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Investigating the Dynamic Interactions of Rapidly Growing Precocial Shorebird Chicks

Luke R. Wilde

INVESTIGATING THE DYNAMIC INTERACTIONS OF RAPIDLY GROWING PRECOCIAL SHOREBIRD CHICKS

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Luke R. Wilde

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Accepted by:

Nathan R. Senner, Director of Thesis

Rose J. Swift, Reader

Carol Boggs, Reader

Tracey L. Weldon, Interim Vice Provost and Dean of the Graduate School

DEDICATION

For my family.

Dad, your unbound dedication to your sons and naturally curious mind have made a world of difference in my life. Mom, your loving support, patience, and infectious courage have helped me to last the hard times and celebrate the good. William, your passion for science education and equity have been a beacon for me as I develop my own career; and Mary Gail and Geno and Jane and Mike, our adventures in the wilds of Montana instilled in me a love for the natural world; you are my role models of working to make a difference, but always making time for family.

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ABSTRACT

Organisms in dynamic environments must continually reassess the cost-benefit trade-offs of their interactions and adjust their behaviors accordingly. Nevertheless, ecological research often takes a 'snapshot' approach to studying interactions across sample locations and timepoints. Investigating ecological interactions in this way can miss important information about the influence spatiotemporal context has on the scale and direction of their effects. Longitudinal studies that follow individuals can elucidate how changing contexts affect an individual's ecology while deepening our understanding of adaptive behavior. However, determining how context influences the effect of an interaction requires it be measured across a range of spatiotemporal conditions. Studying an animal's ecology during periods of rapid change, such as early life development, could be a means of observing an interaction across multiple contexts on a short timescale. As animals grow, their susceptibility to predators, their foraging efficiency, and their energetic needs change because of their increasing body size and life experience. Studying species during early life therefore provides a tractable way to observe how animal behaviors change spatiotemporally. I studied Hudsonian godwit (*Limosa haemastica*) chicks in southcentral Alaska to learn how variable predation risk and resource demands affect their movements and early life survival. In my first chapter, I quantified the effect of stage-specific predation by colonial mew gulls (*Larus canus*) on godwit grouping decisions. Gulls provide umbrella protection for godwit nests but are the main predator of young godwit chicks. I found that by adjusting their association with

gulls according to spatiotemporally variable predation risk, godwits optimize the trade-offs of grouping with gulls during chick development. Then, in my second chapter, I found that the effects of resource availability changed throughout godwit development, whereby low-quality resources have stronger effects on a chick's survival as they grow larger. Further, I demonstrate that accounting for a population's age-structure strengthens the link between resource availability and reproductive success by accurately modeling a consumer's energetic needs. Together, my research underscores the importance of spatiotemporal context on ecological interactions and illustrates how studying intraindividual variation can deepen our understanding of the processes affecting animal behavior and population dynamics.

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CHAPTER 1

INTRODUCTION

Free living organisms experience a wide breadth of ecological interactions relevant to their lifetime fitness (Chamberlain et al. 2014, Cassidy et al. 2020). In living communities, predators, their prey, and con- and heterospecific competitors all interact in space and time and among habitat types (Schmitz et al. 2017). However, while some interactions are more predictable than others, recent work has uncovered the ubiquitous influence that spatiotemporal context has on the scale and direction of an interaction's effects (Palmer et al. 2017, Smith, 2019, Cusack et al. 2020). As a result of this variation, whether a given behavior is optimal – i.e., minimizes the costs and maximize the benefits – depends on the environmental and spatiotemporal context in which it occurs (Ferrari et al. 2019). Understanding how the costs and benefits of a given interaction change with spatiotemporal context is key to identifying optimal behaviors (Chamberlain et al. 2014, Palmer et al. 2017) but making an accurate assessment of the trade-offs involved remains a substantial challenge.

In the dynamic environments that wild animals inhabit, the pressure to respond to the shifting trade-offs of a species' interactions strongly influences individual- and population-level processes (Krebs 1980, Hancock and Milner-Gulland 2006). To survive and reproduce, animals must continuously assess their environments and adjust behaviors to balance the costs and benefits of their interactions in an ever-changing world. Nevertheless, most of ecological research adopts a 'snapshot' approach to studying

interactions across sample locations and timepoints (Schlägel et al. 2019). However, investigating animal interactions in this way can miss important information about how their effects vary among contexts. Given the propensity for context-dependent outcomes of behaviors and interactions, the conclusions drawn under this paradigm may apply to a small range of potential conditions under which interactions can occur, and thus fail to address the larger range of possible outcomes (Ferrari et al. 2019, Wirsing et al. 2020). Drawing broadly applicable conclusions about an interaction's effect requires that it be observed across a range of conditions, but this is often difficult and rarely achieved.

Studying an animal's ecology during periods of rapid change, such as early life development, could be a means of observing their interactions across multiple contexts within a short time span. Ontogeny exerts a major influence over the social and trophic (e.g., predation, foraging) behaviors that animals perform (Pessarrodona et al. 2019). As animals grow, their susceptibility to predators (Fuiman 1994), their foraging efficiency (Ortiz et al. 2019), and their energetic needs (Williams et al. 2007, Yang and Rudolf 2010) change because of their increasing body size and life experience. Additionally, a species' social interactions can change as a function of their age, as in the case of associations with potential predators of young, but not older, individuals (Dugatkin and Godin 1992, Zamora-Camacho et al. 2018). Longitudinal studies that monitor the effects of the interactions of neonatal individuals through space and time may thus clarify the source of inter- and intraindividual variation in populations and deepen our understanding of adaptive behavior.

Shorebird chicks are precocial and self-feeding (Lack 1968), but adults 'tend' broods (i.e., family unit) throughout most of the pre-fledging period (i.e., pre-flight

period; Walker et al. 2011). Over the short breeding season, chicks grow rapidly and achieve high mobility (Tjørve 2007, Williams et al. 2007), so that the interactions that shorebird chicks experience change substantially over the course of development. For instance, the predators (Colwell et al. 2007, Schekkerman et al. 2009), preferred prey (Schekkerman and Boele 2009), and social behaviors that chicks exhibit change as they grow (Larsen and Moldsvor 1992, Dreitz 2009), in part because of changing size-dependent risks and increasing movement capabilities over time. Therefore, investigating how the effects of the interactions shorebird chicks experience change over the course of development will likely provide insights into the context-dependency of animal interactions.

I studied the survival and behavioral effects that trophic (i.e., foraging, predation) and social interactions have on Hudsonian godwit chicks (*Limosa haemastica*; hereafter, 'godwits') in southcentral Alaska. In the two main chapters that comprise my thesis, I address how variable predation risk and resource demands affect godwit movements and early life survival. For this work, I used a long-term dataset (2009–2019) on the movements, survival, and growth of godwit chicks during the pre-fledging period (~ 28 d; Tjørve 2007, Walker et al. 2011) and daily records of the abundance and per-capita size of terrestrial invertebrates, godwit chicks' main prey. Additionally, I used data collected since 2014 on the distribution and phenology of colonial mew gulls (*Larus canus*; hereafter, 'gulls').

In my first chapter, I investigated how the changing costs and benefits of con- and heterospecific associations affects animal grouping decisions using the godwit-gull system as a case-study. The theory around animal grouping supposes that animals join

associations with con- or heterospecifics to avoid costs associated with competition, risk, and misinformation (Dugatkin and Godin 1992, Zamora-Camacho et al. 2018). However, this paradigm still assumes that the risks associated with a given interaction are constant, which is not always the case. For instance, protective nesting associations, such as that formed between godwits and gulls, can have different outcomes depending on the state of development (Haemig 2001, Quinn and Kokorev 2002). While godwits receive indirect protection of their nests from the gull colony, gulls, a main chick predator, depredate young godwit chicks (Swift et al. 2018). Godwits may be able to move away from the gull colony while gulls pose a threat to chicks, but by doing so may be exposed to more variable risk from generalist predators and rely upon conspecifics to offset the costs of gull avoidance. By monitoring the survival and space use of godwit broods with respect to con- and heterospecifics, I found that godwits adjusted their association with gulls according to spatiotemporally variable predation risk. Meanwhile, godwits maintained consistent associations with conspecific broods regardless of their age or density. Therefore, my results provide an example of how animals contend with changing conditions and the role that spatiotemporal context plays in shaping animal grouping behaviors (Larsen and Grundetjern 1997, Mönkkönen et al. 2007).

In addition to predation, godwit chicks also face risks of starvation or malnutrition because of mismatching with ephemeral prey resources. In my second chapter, I investigated the individual- and population-level responses of godwit chicks to phenological mismatching. Using continuous monitoring of godwit chicks and their invertebrate prey during the pre-fledging period, I tested the hypothesis that consumer demands affect the consequences of mismatching by incorporating age-structure in my

analyses. I found that godwit chicks had reduced survival and growth because of lower resource abundance, but the survival effects of low-quality resources intensify as chicks age and require more resources. Then, at the population level, I found that modeling consumer demand according to the population's age-structure improved predictions of annual fledging rates and explained interannual variation in godwit reproductive success better than alternatives based on resource information or temporal asynchrony alone. The results of this chapter suggest that the degree of the mismatch and when individuals experience reduced resource availability affects the consequences for both individuals and consumer populations (Yang and Rudolf 2010, Kerby et al. 2012).

With these two studies, I address how changing conditions affect the behaviors animals exhibit and the effects of their interactions at the individual- and population-level. Being one of the fastest declining species in North America (Rosenberg et al. 2019), research into the processes that affect godwit populations will be invaluable under predicted scenarios of future climate and environmental change.

CHAPTER 2

BEHAVIORAL ADJUSTMENTS IN THE ASSOCIATIONS OF A PRECOCIAL SHOREBIRD MEDIATE THE COSTS AND BENEFITS OF GROUPING DECISIONS

Abstract:

Animals weigh multiple cost-benefit trade-offs when making grouping decisions. The cost-avoidance grouping framework proposes that group density, information quality, and risk affect an individual's preference for conspecific and heterospecific groups. This assumes the cost-benefit balance of a particular grouping is constant, however, which is not necessarily true. Investigating how spatiotemporal context influences grouping choices is therefore key to understanding how social animals contend with changing conditions. Changes in body size during development lead to variable conditions for individuals over short timescales. Hudsonian godwits (*Limosa haemastica*), for instance, form a protective nesting association with a major predator of young godwit chicks, colonial mew gulls (*Larus canus*). Godwit broods may avoid the gull colony when chicks are susceptible to gull predation but likely experience higher risk from alternative predators as a result. Associating with conspecifics could allow godwits to buffer these costs but requires enough other broods with whom to interact. To determine how age-dependent predation risk and conspecific density influence godwit grouping behaviors, we first quantified the time-dependent effect of con- and heterospecific interactions on the risk of death in godwit chicks. We then determined how godwit density and chick age

(i.e., gull predation risk) affected their associations with con- and heterospecifics. We found higher survival rates in godwit chicks that remained close to conspecifics, hatched earlier, and avoided gulls. Additionally, godwit broods avoided gulls when godwit densities were high and early in development, but always maintained loose associations with conspecifics. We identified how individuals can optimally shift with whom they group according to risks that vary spatiotemporally. Investigating the effects of a species' ecological interactions across spatiotemporal contexts in this way can shed light on how animals adjust their associations according to the costs and benefits of each association.

Keywords:

protective association; heterospecific grouping; Cox proportional hazard; *Limosa haemastica*

Introduction:

Animal grouping behaviors affect the structure of ecological communities (Mönkkönen et al. 2007). Groups form around high-quality habitats or as refuges from predation risk, but the costs and benefits of grouping can vary depending on the environment (Fitzgibbon 1990, Gil et al. 2017). For instance, grouped individuals have reduced risk of predation and increased foraging efficiency (Pulliam 1973, Gil et al. 2018), but high group densities can lead to competition (Beecham and Farnsworth 1999, Gil et al. 2017). Additionally, while groups promote shared information about resources and risks (Sridhar et al. 2009), the concentration of individuals can attract predators (Fletcher 2006). Behaving optimally requires that animals weigh multiple trade-offs when making grouping decisions (Mönkkönen et al. 2007). An accurate cost-benefit assessment is therefore necessary to

understand how social animals should contend with changing conditions, but monitoring these across both space and time remains a challenge (Elmhagen et al. 2010).

Many species can group with both con- and heterospecifics (Sridhar and Guttal 2018), but each grouping can come with distinct trade-offs. Conspecific groups are hubs of habitat quality information and refuge from predation risks (Fletcher 2006). However, while the information produced by conspecifics is highly relevant to the individuals in the group, conspecific groups have higher competition among individuals than do mixed-species groups (Goodale et al. 2020). Heterospecific groups, on the other hand, avoid some of the competition costs of conspecific groups while providing a comparatively broader diversity of predator and resource detection capabilities (Sridhar and Guttal 2018). Nevertheless, because a broader range of information is relevant to heterospecific groups as a whole, some individuals may be exposed to higher rates of misinformation (Magrath et al. 2015). Taken together, each species' population density and the value of the information produced by potential groups greatly influence which groups are optimal in each environmental context.

Neither con- nor heterospecific groups are static, though, and species frequently transition between the two groups with single- or multiple-species (Larsen and Grundetjern 1997). The 'cost-avoidance grouping' framework (Trillo et al. 2019, Goodale et al. 2020) lays out three criteria that should determine when it is optimal for individuals to associate more strongly with hetero- than conspecifics: (1) when conspecific groups become too dense or are rarely encountered (Fig. 2.1a; Doligez et al., 2003), (2) when the quality of heterospecific information surpasses that provided by conspecifics (Fig. 2.1b; Meise et al., 2020), and (3) when heterospecifics do not pose a

direct danger (Quinn and Kokorev, 2002; Fig. 2.1c,d). For instance, impala (*Aepyceros malampus*) frequently group with other ungulates (e.g., Thompson's gazelles, *Eudorcas thomsonii*) and avoid lions (*Panthera leo*), but they also join olive baboon troops (*Papio anubis*), a frequent predator of impala calves, when in the presence of other top-predators, such as cheetah (Kiffner et al., 2014).

In its current form, however, the cost-avoidance grouping framework assumes that the costs and benefits of a particular grouping are constant through time. Interactions between competitors and predator-prey pairs change along with conditions. This is especially true for heterospecific associations in which one species may occasionally pose a threat to the other, such as protective associations and resource provisioning relationships. In these cases, the likelihood of a negative or positive outcome are highly context-dependent (Quinn and Kokorev 2002, Morosinotto et al. 2012, Prugh and Sivy 2020). For instance, in protective nesting associations, the likelihood of predation by the 'protector' species can depend on the abundance of alternative prey (Larsen and Grundetjern 1997) or developmental stage of the 'protected' species (Haemig 2001, Morosinotto et al. 2010). By ignoring variable risk within heterospecific interactions across space and time (Willems and Hill 2009), our current understanding of the factors influencing grouping choices may miss important details about how the cost-benefit threshold can change with the spatiotemporal context (Fig. 2.1e,f; Ortiz et al., 2019).

One way to capture interactions across many contexts is by studying a species' ecology during periods of rapid change, such as early life development. Changes to the scale and direction of ecological interactions over the course of ontogeny are ubiquitous across taxa (Yang and Rudolf 2010), but these changes are most clear in size-structured

interactions like predation (Yamaguchi and Kishida 2016). Shorebirds are a case-in-point: shorebird chicks are highly precocial and exhibit rapid growth and mobility changes over short timescales (Engström-Öst and Lehtiniemi 2004, Królikowska et al. 2016). As a result, the sources and absolute levels of predation risk from certain predator classes (e.g., gape-limited predators) varies predictably as chicks age (Dreitz 2009, Schekkerman et al. 2009). Additionally, shorebirds exhibit a wide array of grouping behaviors with con- and heterospecifics, but the degree to which these change in response to predation risks has rarely been considered (see Larsen and Grundetjern, 1997, Dreitz, 2009). Studying the factors influencing the social behaviors and survival of shorebird chicks could therefore provide important insights into how variable risks affect a species' interactions across environmental contexts.

Hudsonian godwits (*Limosa haemastica*; hereafter 'godwit(s)') are long-distance migratory shorebirds that breed across the Nearctic (Walker et al. 2011). The breeding population in southcentral Alaska forms a protective nesting association with colonial mew gulls (*Larus canus*; hereafter 'gull(s)'). We have previously shown that godwit nests inside gull colonies have higher survival to hatch, but at the cost of increased predation of young chicks (<5 d; Swift et al. 2018). Gulls only prey upon young godwit chicks once their own chicks have hatched and require adult provisioning (Swift et al. 2018), however, meaning that godwit hatch dates could affect the predation risk from gulls. Furthermore, because gulls are gape-limited central place foragers (Väänänen et al. 2016), godwits may spatially avoid nesting gulls when their chicks are small and vulnerable to gull predation.

Once outside of the colony however, godwit broods (i.e., the avian family unit) are exposed to generalist predators who, together with gulls, account for 87% of chick mortalities (Senner et al. 2017). Godwits may contend with these variable sources and levels of predation risk by remaining near other conspecifics, a behavior commonly observed in other precocial species (Eadie et al. 1988, Larsen and Moldsvor 1992, Lanctot et al. 1995). The interplay between risk and their associations with con- and heterospecifics is unclear, though. Furthermore, the attrition of godwit broods (i.e., declining density later in the breeding season) could hinder their ability to locate conspecifics with whom to group over the course of the season (i.e., Allee effect; Stephens and Sutherland, 1999).

We investigated how variable predation risk and conspecific density shape the associations godwits form with con- and heterospecifics. To demonstrate the trade-offs that godwits encounter throughout the pre-fledging period, we studied the influence of godwit densities and age-specific vulnerability to gull predation on godwit chick survival and social behaviors. We first determined how interactions with con- and heterospecifics influenced godwit chick survival. Then, we quantified how the strength of godwits' associations changed with godwit density and chick age. We hypothesized that chick survival relates to con- and heterospecific densities, but that the strength of the association with gulls would be age and density dependent. We thus predicted that godwit broods that remained closer to other godwit broods and in proximity to fewer gulls would improve early chick survival, and that godwit broods would avoid gulls when conspecific densities were high and chicks were young (i.e., vulnerable to gulls). Testing these hypotheses will help clarify how animals adjust their behaviors to changing conditions

and elucidate the effects that population-level processes can have on animal grouping behaviors.

Methods:

Study Area

We monitored the survival and space use of godwit chicks near Beluga River, Alaska (61.21°N, 151.03°W; hereafter, 'Beluga') from early-May to mid-July (μ = 78 days) during three study periods: 2009–2011, 2014–2016, and 2019. We divided the study region into two plots – North (5.5 km^2) and South (1.2 km^2) – separated by 7-km of boreal forest (Appendix A: Fig. A.1). Both plots contain freshwater ponds, black spruce (*Picea mariana*) outcroppings, and low vegetation (Swift et al. 2017a), and each plot hosts a large, centrally located gull colony (North: $\overline{x}$ = 66 nests, range = 55–77, South: $\overline{x}$ = 51, range = 41–61).

Nest detection and monitoring

We located godwit nests while surveying the extent of the plots every 2–3 days using behavioral observations and opportunistic encounters. We floated godwit eggs to estimate hatch date and monitored nest survival every 2–3 days (Liebezeit et al. 2007). We transitioned to daily visits once eggs showed pipping or starring.

In 2015, 2016, and 2019, we located all gull nests on both plots. Gulls are the most abundant breeder in the area (Swift et al. 2018) and incubating adults are highly visible on islands within ponds. We estimated the hatch dates of a subset of gull nests ($\overline{x}$ = 21.3 nests, range: 8–45) with repeated nest visits (2015–2016) and egg flotation (2019; Westerskov, 1950).

Godwit chick capture and monitoring

Immediately after hatch, we marked godwit chicks with a unique alpha-numeric flag and USGS metal band placed on the tibiotarsus. We found some broods post-hatch each year (range: 0–4 broods) and opportunistically captured these chicks as well. We estimated the hatch dates of chicks captured opportunistically using published age-specific mass estimates (Senner et al. 2017). Because of the conspicuousness of adult godwits during the chick-rearing phase and the size of the plots, we are confident that we found and monitored all broods each year.

We randomly selected 1–2 chicks from each brood (range: 7–23 per year) for monitoring with radio telemetry. We attached a 0.62g VHF radio transmitter (Holohil Systems Ltd.) to the skin above the uropygial gland using cyanoacrylate glue. Radios and flags were < 3% of a chick's mass at hatch and were unlikely to affect the survival of shorebird chicks (Sharpe et al. 2009, Senner et al. 2017). We relocated each radioed chick every 1–3 d (Appendix A: Table A.1) and recaptured them every 7 d to replace the glue under the radios throughout the pre-fledging period (28–30 d, Walker et al., 2011). We estimated each chick's location with 3–5 azimuths towards the greatest signal strength and converted these to determine each chick's location within 10 m using the program LOCATE (v. 3.34, 2011).

When we did not locate a chick's radio, we walked concentric circles away from that individual's last known location. We presumed a chick was dead if we could not detect a signal after three consecutive days of relocation attempts. Although the average lifespan of our radios was only 21 d (range: 17–33 d; Holohil Systems, 2021), we did not record any radio failures. Furthermore, no chicks that were presumed dead were resighted

later in the season (N.R. Senner, University of South Carolina, unpublished data, 2019). In many cases, when a radioed chick died, other chicks in the brood were still alive (67% of broods). For these active broods without a radioed chick, we opportunistically located adult godwits exhibiting clear parental care behaviors (e.g., alarm calling, flights towards observers; Walker et al., 2011) as a rough estimate of the brood's location (n = 335) for use in later spatial analyses (see *Space use sharing: between godwit broods and with the gull colony*).

Godwit and gull interaction in space and time

To clarify the timing of godwit-gull interactions, we investigated the synchrony between godwit and gull nesting phenologies. We compared the proportion of gull and godwit nests hatched per day of the season using a generalized additive model (GAM) in the package 'gamlss' (Rigby and Stasinopoulos 2005) with a beta distribution and logit-link function using program R (v.4.0.3; R Development Core Team, 2020).

Adult godwits tending a brood partially guide the chicks' movements, but chicks exhibit independence at hatch (Colwell et al. 2007, Schekkerman and Boele 2009). Additionally, godwit broods freely traverse other godwits' nesting territories throughout the pre-fledging period (RJ Swift, U.S. Geological Survey, unpublished data, 2019). Nonetheless, a parent's choice of nest may influence where chicks move, especially early in development when chick movement may be limited (Schekkerman and Boele 2009). We therefore investigated the degree to which natal nest site characteristics constrained chick movements and affected the associations godwit chicks formed with con- and heterospecifics. First, we quantified both the distance broods moved between consecutive relocations and the net-squared displacement from their nest using the package

'adehabitatLT' (Calenge 2006). Then, we built three separate univariate linear mixed-effect models (package 'lme4'; Bates et al., 2020) and tested the effect of nest site characteristics and a chick's movement by regressing the [1] distance to nearest conspecific brood, [2] number of gull nests within 200 m, and [3] distance to the gull colony centroid during the nest stage on the same metrics during the brood stage. We included random intercepts for [4] study plot and [5] brood ID and a random slope term for [6] chick age.

Chick survival

We examined the influence of six covariates on daily chick survival. First, we included estimates of conspecific interactions and site-level density – [1] nearest neighbor distance (i.e., the distance between tagged chicks) and the [2] daily brood density (Appendix A: Table A.2) – calculated separately for each plot. We calculated nearest neighbor distances using the 'spatstat' package (Baddeley and Turner, 2005). Second, we estimated the effect of [3] nest hatch date, which is indicative of nesting attempt in shorebirds because of high among-individual synchrony in nest initiation (Swift et al., 2020). Third, we tested for the influence of heterospecific associations at time *t* with the [4] Euclidian distance to the gull colony centroid and [5] number of gull nests within 200 m (Swift et al. 2018). Predators are typically more abundant nearer the forest edge in Boreal regions (Robinson et al. 1995, Lima 2009, Roos et al. 2018). Therefore, while we lacked data on the occurrence of other predator species, we used [6] distance to forest edge as a proxy for their effect.

We built a mixed effect, Cox proportional hazard model (mCPH) to estimate the time-dependent, additive effects of our covariates on chick survival ('coxme'; Therneau,

2020). CPH models estimate the effect of covariate values on the instantaneous risk of death at time *t* with a semiparametric function. The mCPH includes random effects within a frailty model structure (Murray and Sandercock, 2020) and assumes that (1) predictor variables have constant effects, (2) survival probability is cumulative, (3) individuals are censored randomly, and (4) fates are known. By incorporating random intercepts, mCPH models are robust to deviations from a last assumption, (5) independence among individuals. We suspected differences among broods, plot, and study year affected survival. We therefore included [7] study year and [8] study plot as random intercepts, with [9] chick within brood ID as a nested random intercept. Lastly, we confirmed that the proportional hazards assumption of the Schoenfeld residuals was met and that predictors had minimal disproportionality ($p_{global} = 0.85$; Appendix A: Table A.3, Fig. A.2).

We compared hazard coefficients for the main effects (β_i) to the population baseline hazard (β_0) to estimate the hazard ratio (HR, e^{β}), where a predictor decreases risk ('protective') when an HR<1 and increases risk ('hazardous') when HR>1. We used the 3-d average of continuous covariates and rescaled each predictor variable by centering and dividing by two standard deviations following Gelman (2008). We performed model selection using separate multivariate models and calculating Akaike's Information Criterion scores corrected for small sample sizes (AIC_c; Burnham and Anderson, 2002) in the package 'MuMIn' (Bartoń 2015). When no single model had a weight (w_i) > 0.90, we used model averaging and report only the conditional averages (Grueber et al. 2011). We made biological interpretations for predictors with HR confidence intervals that did not include one.

While mCPH offers more robust hazard estimation, it does not allow for cumulative survival estimation (Murray and Sandercock, 2020). We therefore elected to use a simplified model to estimate the effects of predictors in our top mCPH model on cumulative survival. Cumulative survival estimation requires categorical predictors. We used the Levallée–Hidiroglou method from the package 'stratification' (Baillargeon and Rivest 2011) to identify three levels within each predictor variable. The Levallée–Hidiroglou method iteratively estimates within-group variation to identify the most likely cut-off boundaries among a specific number of groups specified by a K-means algorithm within the numerical data (Gunning and Horgan 2007). Finally, we built univariate models to estimate chick survival to fledging with a 95% CI for each level of our selected predictor variables, with brood ID as the cluster term ('survival'; Therneau, 2015).

Space use overlap between godwit broods and with the gull colony

To determine how a brood's associations with other broods and the gull colony changed throughout development, we estimated the amount of space use overlap using kernel-based home range estimators. Given our low sample size of brood relocations, we divided brood locations into two periods – ≤14 d (early development) and >14 d (late development) – as 14 d was the oldest age chicks were found depredated by gulls (see *Results*). Within each period, we calculated each brood's kernel utilization distribution (KUD) as an estimate of brood home range (Schmitz et al. 2017). KUD estimates from similarly small sample sizes can overestimate the kernel area (Fleming and Calabrese 2017); however, given the relatively short distances godwit chicks traveled between relocations (all ages: $\bar{x}$ = 372.80 ± 343.90 m, n = 492), we are confident that any bias was minimal.

We constructed KUDs for godwit broods from the chick triangulations or brood resights, and for the gull colony from each year's gull nest locations using the package 'adehabtiatHR' (Calenge, 2006), with a grid factor of 30 and the default smoothing factor (range: 0.7–2.0). Because only one godwit brood survived past 14 d in the South plot in all seasons and only one survived in the North plot in 2014, we excluded all South plot broods and all 2014 broods from this analysis. For years when gulls were not fully monitored (2009–2011, 2014), we approximated nest locations from the average nest locations in monitored years. We treated gull nests as locations and the colony as an individual. The 95% KUD for the gull colony in each season closely resembled the minimum bounding geometry.

We calculated the Utilization Distribution Overlap Index (UDOI) to estimate the pairwise amount of space use sharing (i.e., overlap) between godwit broods and between each godwit brood and the colony (Fieberg and Kochanny 2005). While similar indices of spatial overlap range from 0 (no overlap) to 1 (complete overlap), UDOI incorporates information on space use and can be >1 (high space use sharing). We calculated four UDOI values for each brood – between broods (conspecific), as well as between broods and the colony (heterospecific) – in early and late development with bootstrapped (100 iterations) 95% CIs.

Density- and age-effects on heterospecific and conspecific spacing

We tested if the godwit population in Beluga has declined over the study period and, if so, what effect that decline may have had on the associations godwits formed. To determine if the godwit population declined over time, we used a linear regression to estimate the change in observed daily densities of godwit broods in our study site across

[1] study years. We included [2] Julian day and [3] Julian day^2 as blocking variables to account for variation in season length.

To determine whether brood density or chick age explained the associations broods formed with con- and heterospecifics, we used mixed-effect generalized additive models (GAMMs) with a gaussian error-term and identity link. The Pearson's correlation between age and density was low ($r = -0.14$, $p<0.05$). We therefore elected to measure their effects in the same model. We estimated the additive effects of [1] chick age and [2] brood density on both the nearest neighbor distance and distance to the gull colony centroid in separate models, each with [3] brood ID as a random slope random intercept. We included [4] quadratic terms for chick age to test for non-linear effects throughout development.

Data used in this study are available from the Dryad Digital Repository https://datadryad.org/stash/dataset/doi:10.5061/dryad.x95x69pfq.

Results:

We monitored the survival of 128 godwit chicks from 102 broods throughout the study period (2009–2011: $n = 60$; 2014–2016: $n = 46$; 2019: $n = 22$). We located each radio tagged chick an average of 4.3 times (SD = 2.71, range: 1–19; $n = 778$), generally 1.07 days apart (SD = 0.49 d, range: 1–4 d), and each surviving brood an average of 11 times (SD = 8.89, range: 1–39; $n = 428$), generally 0.6 days apart (SD = 0.82 d, range: 0–2 d). Across all sample years, 24.2% of radioed chicks survived to fledging (i.e., 28 days; Walker et al., 2011), with an average life span of 11.9 d (SD = 8.03 d). Fledging success varied across years but, on average, 27% of broods fledged at least one chick (range: 0–50%).

Godwit and gull interactions in space and time

In 2015, 2016, and 2019, we located, on average, 115 gull nests (North: range = 55–77, South: range = 41–61) and estimated the hatch dates of 29 gull nests in each season (range: 10–44). Despite gulls arriving to Beluga several weeks earlier than godwits (Swift et al. 2018), gull hatch was highly synchronous with godwit hatch (difference in hatch dates: β = -0.14 ± 0.16 days, 95% CI = -0.45, 0.18, n = 119; Fig. 2.2).

Godwit chick movements were not related to nest site location. Radio tagged godwit chicks moved on average 373 m between relocations (SD: 344 m, range = 36–1,311 m; Appendix A: Table A.4) regardless of age ($F_{1,364}$ = 0.86, p > 0.35). Chicks, on average, were relocated 423 m from their nest (SD: 422 m, range = 22–1,445 m). However, the associations godwit broods formed were weakly related to their nest site location, but varied considerably with chick age and among broods. Both a brood's distance to the nearest conspecific nest (β = 0.56 ± 0.23; 95% CI = 0.12, 0.94; R^2_m = 0.05, R^2_c = 0.65; n = 492) and the distance to the gull colony centroid (β = 0.42 ± 0.17; 95% CI = 0.09, 0.76; R^2_m = 0.05, R^2_c = 0.77; n = 790) weakly increased with the distance from the nest site to the nearest conspecific nest and gull colony centroid, respectively. The number of gull nests within 200 m of a brood's location did not correlate with the number of nearby gulls during the nesting phase (β = 0.20 ± 0.13; 95% CI = –0.05, 0.47; R^2_m = 0.01, R^2_c = 0.63). In each case, the random intercept terms brood ID (n = 89) and chick age had 13- to 63-times larger influence over a chick's association with con- or heterospecifics than the nest site characteristics.

Chick survival

From 2009–2019, we recovered the carcasses (n=30) or plucked radios (n=16; e.g., skin and gauze attached) from 58% of all presumed chick mortalities (n=79). Of the instances in which we found a carcass or radio, 73% (n=34) were within the gull colony, and 56.5% were on or within 25 m of an active gull nest (n=26) and therefore likely directly attributable to gull predation. No godwit chicks died from gull predation after they reached an age of 14 d, but 60% of chicks killed by unknown predators died after 14 d (Appendix A: Fig. A.3).

Our top mCPH model included nearest neighbor distance, brood hatch date, number of nearby gull nests, and distance to the gull colony centroid (n = 451 observations, 956 iterations, w_i = 0.22, Appendix A: Table A.5). A chick's risk of death increased by 16% with each additional 100 m of distance to its nearest conspecific neighbor (Table 2.1). Chicks that remained close (< 291 m) to conspecifics had 7–16% higher survival than those maintaining moderate or long distances respectively (Fig. 2.3, far left). Additionally, later hatch dates increased a chick's risk of death by 11.6% with each day they hatched after 31 May. Chicks that hatched before 4 June had 18–36% higher fledging success than those hatched after 5 or 10 June respectively (Fig. 2.3, middle left).

Chick survival decreased with greater gull densities. Each gull nest within 200 m increased a chick's risk of death by 6%, such that chicks with <3 nearby gull nests had 26–36% higher survival than those with greater numbers of nearby gull nests (Fig. 2.3, middle right). Finally, each additional 100 m from the gull colony reduced a chick's risk

of death by 8%. Chicks outside of the colony (i.e., >637 m from the centroid) had 26% better survival probabilities than those inside the colony (Fig. 2.3, far right).

Space use overlap between broods and with the gull colony

During both early and late development, broods occupied similarly sized 95% KUD areas (<14 days: 1.87 ± 0.23 km^2, n = 44, >14 days: 1.82 ± 0.42 km^2, n = 18, Appendix A: Table A.4). Godwit broods had moderate space use sharing with gulls in early development (0.32 ± 0.01; 95% CI = 0.25, 0.40, n = 44; Appendix A: Fig. A.4), but high space use sharing in late development (0.68 ± 0.04; 95% CI = 0.41, 1.05, n = 18). Meanwhile, broods had consistently moderate levels of space use sharing with conspecifics in both early (0.32 ± 0.08; 95% CI = 0.27, 0.37, n = 348) and late development (0.24 ± 0.01; 95% CI = 0.17, 0.31, n = 58).

Density- and age-effects on heterospecific and conspecific spacing

The maximum godwit brood density occurred on 12 June (SD = 3.31 days) and did not differ among years ($F_{1,5}$ = 0.90, p = 0.39). However, the number of active broods in Beluga on any given day declined over the course of the study (β = -0.52 ± 0.06; 95% CI = -0.39, -0.64, R_{adj}^2 = 0.58, n = 294).

The distance between godwit broods and the gull colony centroid varied with age and conspecific density. Godwit broods avoided the gull colony at higher brood densities (β = 17.49 ± 6.14 m; 95% CI = 5.69, 29.28; n = 421; Fig. 2.4a). Concurrently, a chick's distance to the gull colony was curvilinear throughout development, whereby young chicks avoided the gull colony until 14 d but moved closer to the colony thereafter (linear: β = 37.66 ± 7.98; 95% CI = 22.34, 52.98; quadratic: β^2 = -1.37 ± 0.36, CI: -0.69, -

2.06; Fig. 2.4b). Brood ID explained 52% of the variance in a chick's association with gulls, while age (6%) or density (1%) explained little.

Conversely, the distance between conspecific broods was not well predicted by brood density ($\beta = -4.70 \pm 3.27$; 95% CI =-10.98, 2.56; $n = 421$; Fig. 2.4c) or chick age (linear: $\beta = 3.77 \pm 4.59$; 95% CI =-5.06, 12.59; quadratic: $\beta^2 = -0.16 \pm 0.21$; 95% CI = -0.55, 0.24; Fig. 2.4d). Again, brood ID explained 39% of the variance in the conspecific association, while age and density explained 0.5% and 0.6%.

Discussion:

A growing consensus suggests that the effects of heterospecific interactions vary in their scale and direction spatiotemporally (Durant et al. 2005, Chamberlain et al. 2014). Nevertheless, the cost-avoidance grouping framework assumes that the costs and benefits of a given association are constant for a given interaction (Larsen and Grundetjern 1997, Meise et al. 2020). To address this potential oversight, we investigated how variable risk affects animal grouping behaviors by monitoring a heterospecific association whose costs and benefits change spatiotemporally. Using observations of the association between Hudsonian godwits and mew gulls over godwit chick development, we provide evidence of behavioral adjustment in grouping behavior according to variable predation risk. We found that godwit chick survival improved with stronger conspecific associations, earlier hatch dates, and lower gull densities. We also found that godwit broods weakened their association with gulls when chicks were young and when conspecific densities were high, but maintained consistent associations with conspecifics regardless of brood density or age. Our results provide insights into the role of adaptive grouping behaviors for animals contending with changing environmental conditions, specifically potentially dangerous

heterospecifics (Morosinotto et al. 2012, Tórrez-Herrera et al. 2020). Investigating the effects of a species' ecology within a spatiotemporal context can thus shed light on how animals optimally adjust their associations according to the changing costs and benefits of each interaction (Sridhar and Guttal 2018).

Shifting associations as an adaptive predator avoidance behavior

Prey species adjust their space use in response to some predators while tolerating others (Willems and Hill 2009). Accordingly, we found that godwit broods avoided gulls early in development and when more conspecifics were available to group with. In fact, godwit space use had 112% less overlap with the gull colony when chicks were susceptible to gull predation than when they were not. Species that group with dangerous heterospecifics may thus reduce the strength of the association until the cost-benefit balance favors grouping (Quinn and Kokorev 2002, Morosinotto et al. 2010, Kiffner et al. 2014). A similar mechanism may allow social species in general to optimally adjust the strength of their associations depending on the trade-offs presented by specific grouping behaviors (Larsen and Grundetjern 1997, Bicca-Marques and Garber 2003, Goodale et al. 2020).

In contrast to the godwit-gull association, godwits maintained loose associations with conspecifics at all ages and brood densities. Conspecific associations that are favored by selection regardless of their density can indicate high anti-predator benefits (Pulliam 1973, Fletcher 2006). Indeed, we observed 7–23% higher survival in chicks with nearby conspecific neighbors. Still, while the associations we observed between godwit broods were too weak to be considered grouping in the strictest sense, they nevertheless likely facilitate the anti-predator benefits typical of groups. For instance,

adults of similar shorebird species are known to broadcast risk information with frequent alarm calls and often haze or physically attack predators in groups involving adults from multiple broods (Larsen and Moldsvor 1992). The loose associations godwits formed with other broods may therefore reflect the spatial scale at which information transfers or umbrella protection occurs (Lengyel 2007, Rocha et al. 2016).

The anti-predator benefits that godwits gain from associating with conspecifics are likely most important when they are avoiding the gull colony. In other boreal ecosystems, generalist predators are most abundant close to the forest edge (Lima 2009, Roos et al. 2018). This is likely true for Beluga as well given the predator deterrence of the centrally located gull colony. While we did not measure their abundance directly, generalist predators could account for ≥27% of all chick mortalities and thus constitute a major source of godwit reproductive failure (Schekkerman et al. 2009, Sládeček et al. 2014). Godwits that associate with conspecifics may better navigate the variable risk from generalist predators while avoiding the gull colony and its anti-predator benefits.

If conspecifics can provide anti-predator benefits, however, why do godwits associate with gulls again later in development? We hypothesize that this may be related to two features of the gull colony. First, gulls are both the most numerous (Swift et al. 2018) and most easily located species on our study plots, with adult gulls remaining near the nest site until their chicks are nearly volant (Dornhaus et al. 2006, Gil et al. 2017). Second, the gull colony's predator detection and deterrence capabilities mean the colony remains a consistent source of risk information and protection for godwits – even during chick development (Vermeer and Devito, 1986, Mönkkönen et al., 2007). Therefore, while conspecifics provide alternative sources of anti-predator benefits, returning to

group with gulls is likely optimal once chicks are larger and less vulnerable to gull depredation and as the number of broods dwindles over time.

Predator-prey synchrony intensifies the risk experienced by later hatched chicks

We found strong directional selection on godwit hatch dates, whereby godwit chicks from earlier nests were 18–36% more likely to survive to fledge than later hatched chicks. Size-dependent interactions with predators can enact strong selection on reproductive timing (Fuiman 1994, Start 2020). In this system, gulls only prey upon young godwit chicks once their own chicks have hatched and require adult provisioning (Swift et al. 2018). Therefore, only godwit chicks that hatch later are likely to experience higher predation risk from gulls during the early part of development than earlier hatched chicks. Indeed, godwit chicks that hatched after the median gull hatch date (7 Jun) experience 93% higher risk of death than the earliest godwit nests (31 May). Strong synchrony between predators and their prey is common because predators experience similar abiotic and biotic cues, and even take cues from their prey (Daugaard et al. 2019). As a result, the interplay between predator-prey synchrony and size-dependent risk may interact and broadly influence predation rates.

Survival advantages of earlier hatched chicks are consistent with those documented in other studies of shorebird breeding success (McKinnon et al. 2012), but these are generally attributed to reduced resource availability for later individuals (Saalfeld et al. 2019). We have previously shown that godwit chick body condition and survival both decline with later hatch dates and reduced resource abundance (Senner et al. 2017, Wilde 2021a). Thus, while we did not include analyses of the effects of resource on chick survival in this study, the greater predation risk experienced by later hatched chicks

may act synergistically with resource availability to influence the optimal timing of godwit reproduction.

Importantly, however, both predation risk and resource availability are variable throughout chick development and likely affect the optimal behaviors godwits perform. In this study, godwit chicks were killed by gulls only in the first 14 d of development but were depredated by generalist predators at similar rates throughout the pre-fledging period. Meanwhile, past observations suggest that the effects of resource availability also change over ontogeny, whereby periods of low resource quality reduce a chick's survival more strongly as they age and require more energy (Wilde 2021a). Temporally variable predation risk and resource availability may both influence optimal behavior in godwits, but the degree to which these pressures interact is not well understood. The strength of trophic interactions can depend on their timing in development (Fuiman 1994, Durant et al. 2005). Therefore, monitoring a species' interactions with both their predators and prey, as well as how they shift over time, is likely necessary for understanding how animals optimally respond to changing conditions (Daugaard et al. 2019, Damien and Tougeron 2019).

Conspecific associations in declining species

We found strong evidence of local declines in the population of breeding godwits. Daily densities of godwits on our study plots during the brood-rearing period have declined by 1.5% per year compared to 2009 levels. These results are counter to previous range-wide surveys during the nonbreeding season, which depicted stable populations (Andres et al. 2012, Garcia-Walther et al. 2017). Despite the limited area over which we sampled godwit densities, our findings may be relevant throughout the full godwit breeding range

considering the density-dependent behavioral strategies and survival we have observed in godwits (see also Swift et al. 2020b). For instance, the benefits of conspecific attraction require there be conspecifics with whom to group, which is inherently related to godwit density. Therefore, large-scale population declines may ultimately intensify the effects of brood attrition over the course of the season, leading to earlier thresholds in the season past which conspecific grouping is unfeasible ('Allee effects'; Stephens and Sutherland, 1999). Godwits as a species have been declining at a rate of ~3.4% annually since 1970 (Rosenberg et al. 2019), meaning that similar effects from reduced conspecific densities may be occurring elsewhere across their range as well. Given the benefits of conspecific associations we observed and the role of conspecific signaling in godwit settlement decisions (Swift et al. 2017), godwits across their range may soon face constraints in their ability to group with conspecifics throughout the breeding season.

Conclusions

We showed that the shifting costs and benefits of heterospecific interactions can affect species' grouping decisions. Godwit broods facing multiple sources of predation risk used flexible associations to optimally avoid the costs of both grouping with and avoiding dangerous heterospecifics. Additionally, we show how ontogeny and variation in the timing of the post-natal period can interact to affect the ecological interactions individuals within a population experience during early life. The benefits of social information exchange and interactions among species within mixed-species assemblages thus likely depend on the current balance of costs and benefits of each association (Murray and Magrath 2015; Haak et al., 2020). More generally, variation in the effects of ecological interactions across space and time illustrate the importance of monitoring

potential trade-offs across spatiotemporal contexts before drawing conclusions about optimal behaviors (Durant et al. 2005, Chamberlain et al. 2014).

Table 2.1. Estimated effect of predictor variables from the conditional averages of a time-to-event, mixed-effect proportional hazard model (n = 452; 956 likelihood iterations). Hazard coefficients of standardized predictor variables are reported for comparison among predictors, while unstandardized coefficients are described in the text. Predictors with hazard ratio confidence intervals that do not include 1.0 are considered biologically relevant (bold face).

Predictor[1]	*Relative Hazard (β)*	*Standard Error*	*Hazard Ratio*[2] *(HR)*	*HR 95% CI*
Nearest neighbor distance	**0.958**	**0.233**	**4.112**	**(1.651, 4.118)**
Hatch date	**0.940**	**0.188**	**4.998**	**(1.770, 3.700)**
Number of nearby gull nests	**0.493**	**0.218**	**2.265**	**(1.069, 2.510)**
Distance to forest edge	0.201	0.252	0.799	(0.746, 2.005)
Brood density	-0.223	0.263	0.847	(0.478, 1.340)
Distance to gull colony centroid	**-0.769**	**0.326**	**2.361**	**(0.245, 0.878)**

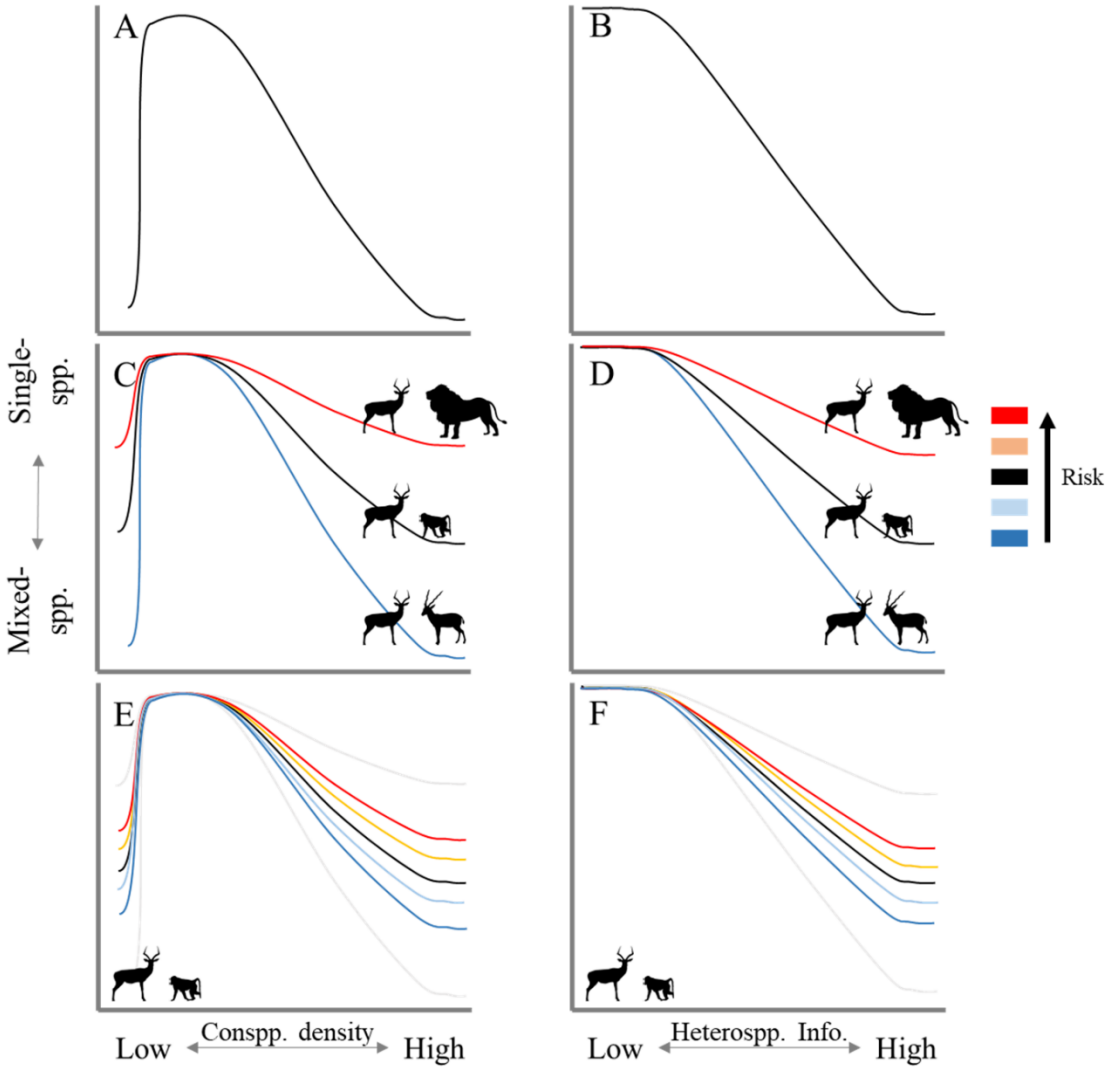

Figure 2.1. The cost-avoidance framework supposes that mixed-species groups are increasingly optimal as (A) conspecific density grow (i.e., competition) or fall (i.e., infrequent encounter) past a cost-threshold or (B) heterospecifics produce higher quality information relative to conspecifics. Additionally, (C, D) mixed-species groups are less likely to form when the risk of the heterospecific interaction (blue is low risk, red is high risk) increases. We propose that for interactions with potentially lethal outcomes (E, F), the cost-benefit thresholds affecting selection for mixed-species groups changes as risk varies (blue is low risk, light blue is moderately low risk, black is moderate risk, yellow is moderately high risk, and red is high risk).

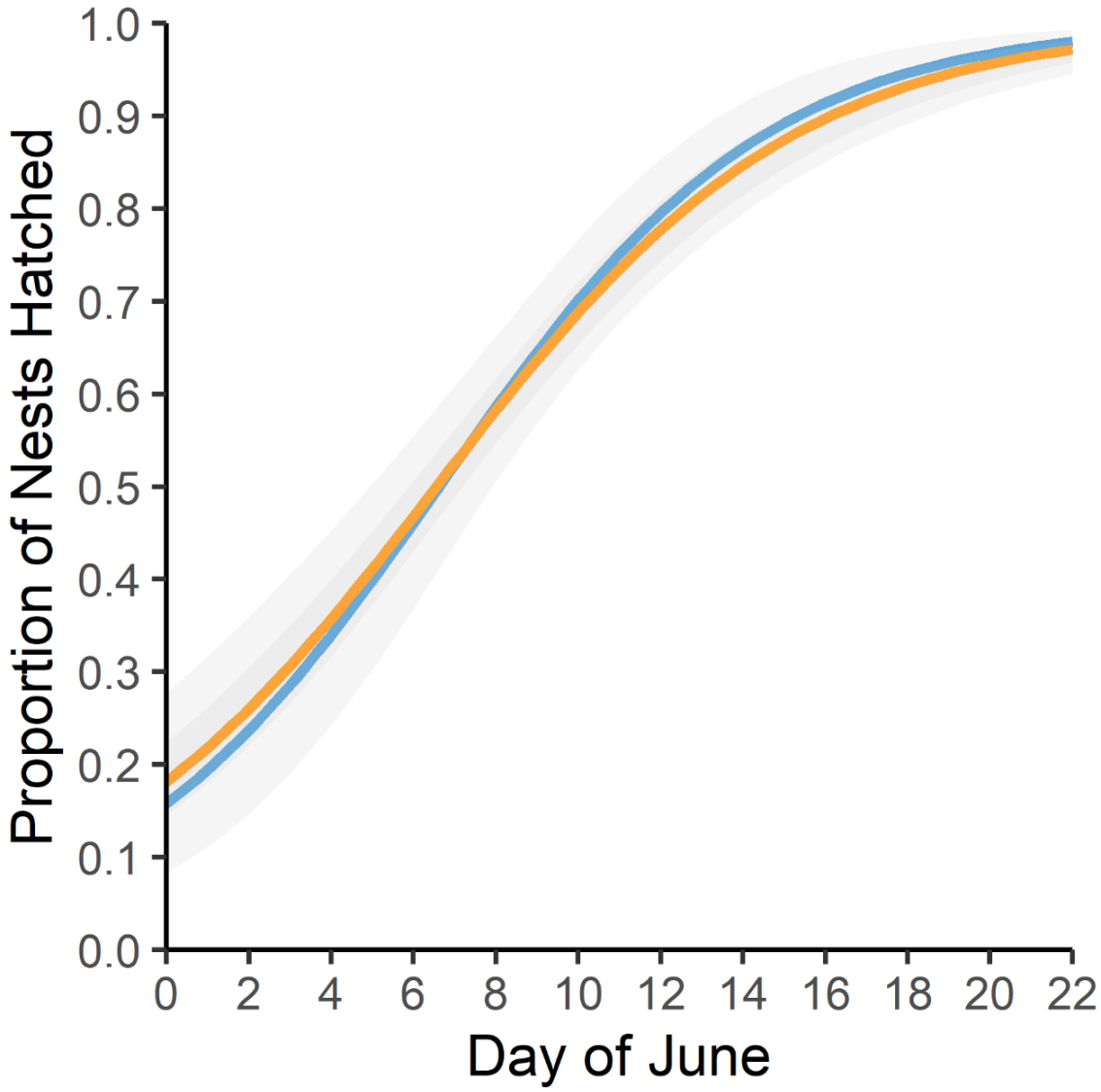

Figure 2.2. Proportion of Hudsonian godwit (orange) and mew gull (blue) nests hatched by each day in June. Estimates are shown with 95% confidence intervals (grey).

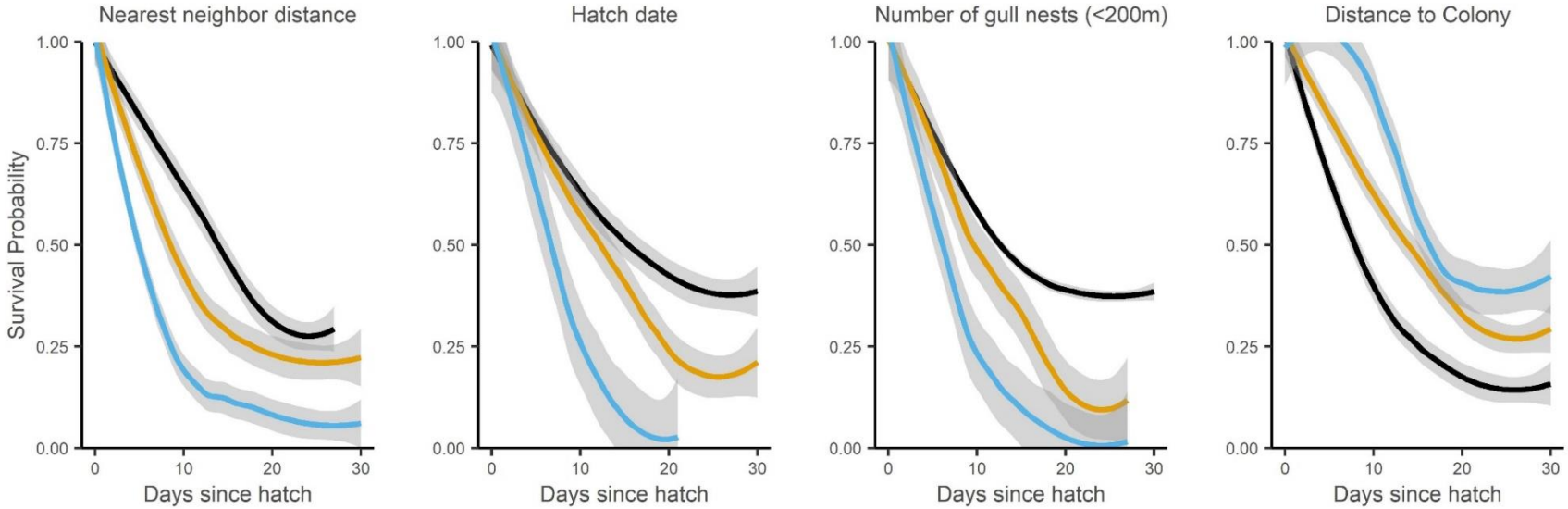

Figure 2.3. Hudsonian godwit cumulative chick survival to fledge (28 days) across categorical levels of (left to right) nearest neighbor distance, hatch date, number of nearby mew gull nests, and distance to the gull colony. Predictor levels were chosen using the Levallée–Hidiroglou method: nearest neighbor: close (black; d<291 meters), moderate (yellow; 291<d<646 m), and far (blue; d>646 m); hatch dates: early (black; before 4 Jun), middle (yellow; 5 Jun–9 Jun), and late (blue; after 10 Jun); number of mew gull nests: few (black; x<3 nests), moderate (yellow; 4<x<8 nests), and many (blue; x>9 nests); and distance to the gull colony: far (blue; d>1119 meters), moderate (yellow; 638<d<1118 m), and close (black; d<637 m). Point estimates are shown (lines) with their 95% confidence intervals (grey)

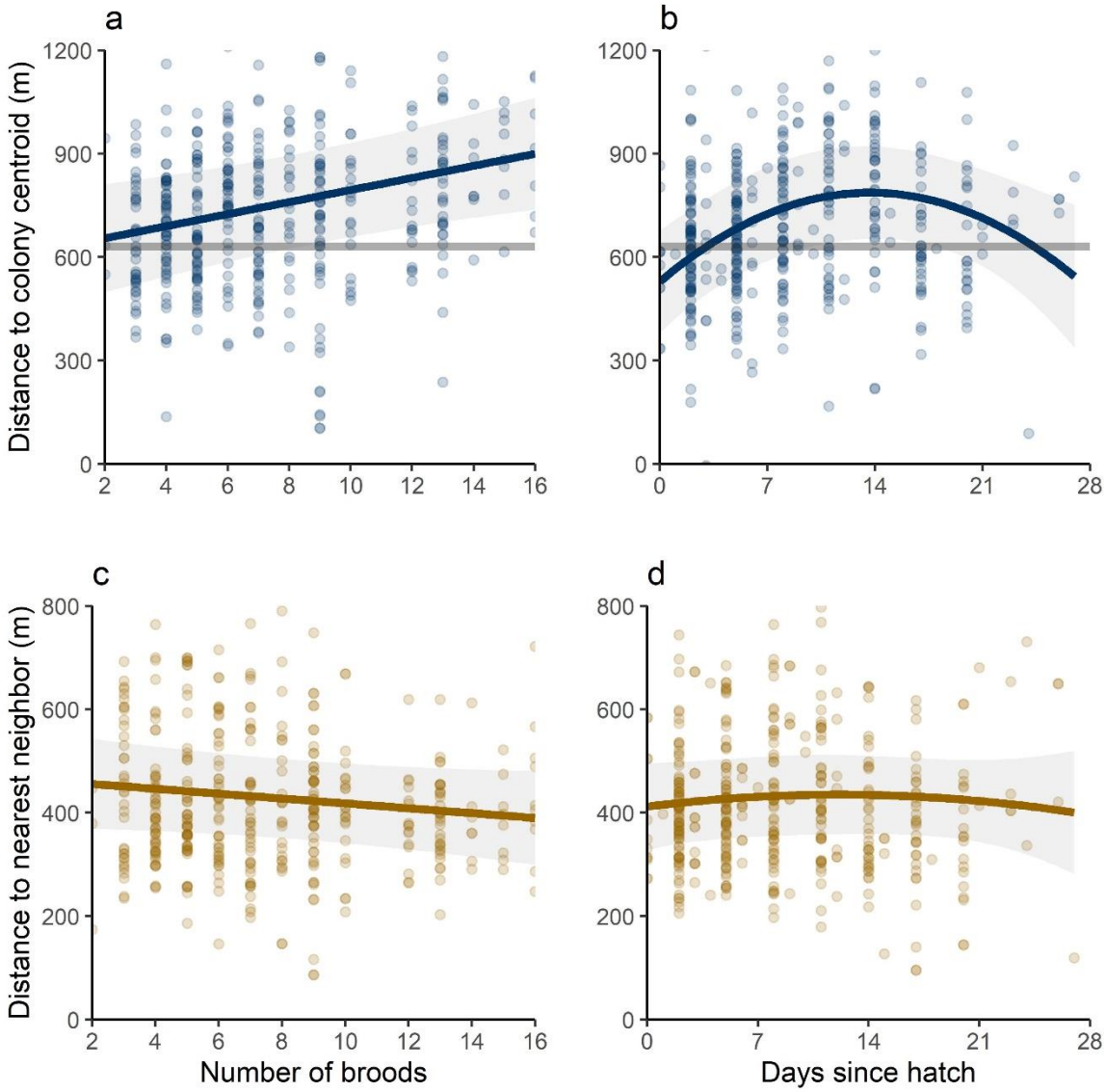

Figure 2.4. Effect of number of Hudsonian godwit broods (i.e., density) and days since hatch (i.e., chick age) on distance to the mew gull colony centroid (a, b; *n*=403) and the nearest neighbor distance between broods (c, d; *n*=403). (a) Distance to gull colony centroid (m) as a function of observed brood densities and (b) chick age during the pre–fledge. The horizontal line represents the mean distance to the edge of the mew gull colony among years (μ=630.23 meters). (c) Nearest neighbor distance (m) as a function of density and (d) chick age. Effects are shown with covariates set to mean. Regression lines are displayed with 95% confidence intervals (grey).

CHAPTER 3

THE ANATOMY OF A PHENOLOGICAL MISMATCH: INTERACTING CONSUMER DEMAND AND RESOURCE CHARACTERISTICS DETERMINE THE CONSEQUENCES OF MISMATCHING

Abstract:

Climate change has caused shifts in seasonally recurring biological events and the temporal decoupling of consumer-resource pairs – i.e., phenological mismatching. Despite the hypothetical risk mismatching poses to consumers, it does not invariably lead to individual- or population-level effects. This may stem from how mismatches are typically defined, where an individual or population are 'matched or mismatched' based on the degree of asynchrony with a resource pulse. However, because both resource availability and consumer demands change over time, this categorical definition can obscure within- or among-individual fitness effects. We investigated the effects of resource characteristics on the growth, daily survival, and fledging rates of Hudsonian godwit (*Limosa haemastica*) chicks hatched near Beluga River, Alaska between 2009 and 2019. To do this, we developed models to identify the effects of resource characteristics on individual- and population-level processes and determine how the strength of these effects change throughout a consumer's early development. We found that at the individual-level, chick growth and survival improved following periods of higher invertebrate abundance but were increasingly dependent on the availability of larger prey as chicks aged. At the population level, annual fledging rates were best explained by a

model including age-structured consumer demand. Our study suggests that modeling the effects of mismatching as a disrupted interaction between consumers and their resources provides a biological mechanism for how mismatching occurs and clarifies when it matters to individuals and populations. Given the variable responses to mismatching exhibited by consumer populations, such tools for predicting how populations may respond under future climatic conditions will be critical for conservation planning.

Keywords:

climate change; Bayesian hierarchical model; ontogeny; mechanistic model; resource availability

Introduction:

Shifts in the timing of recurring biological events (i.e., phenology) are among the best documented effects of climate change on living systems (Parmesan and Yohe 2003). Higher spring temperatures have led to earlier peaks in seasonal resources (e.g., invertebrate biomass; Pearce-Higgins et al., 2005, Tulp and Schekkerman, 2008). Slower rates of phenological advancement at upper trophic levels, however, mean that future climatic conditions will likely lead to a greater decoupling of consumer-resource pairs (i.e., 'mismatching'; Both and Visser, 2001, Both et al., 2009). Despite the theoretical risks imposed by climate-induced mismatching, mismatches do not invariably lead to reduced individual fitness (Dunn et al. 2011, Corkery et al. 2019) or negative demographic consequences for populations (Visser et al. 2012, Reed et al. 2013, Keogan et al. 2020). The inconsistent effects of mismatching may be due to among-individual variation (Reed et al. 2013), although the underlying assumptions of existing mismatch models have also received scrutiny (Visser and Gienapp 2019). Recent studies have

proposed improved methodologies for studying mismatches (Kharouba and Wolkovich 2020), but overcoming the empirical-theoretical disconnect in phenological studies may first require an improved mechanistic framework to help elucidate the degree to which mismatching occurs (Takimoto and Sato 2020).

The match-mismatch hypothesis presents mismatching as the disrupted interaction between consumer demands and resource availability (Cushing 1990). Most empirical studies categorize individuals or populations as either 'matched or mismatched' depending on the synchrony between the timing of a single life-history event and resource availability (Cushing 1974, Visser et al. 1998). Contrary to this categorization, both resource availability and consumer demands vary over time, and being 'matched' does not guarantee that consumers have sufficient food (Saalfeld et al. 2019, Keogan et al. 2020). Rather, changes to continuous resource characteristics like quantity (i.e., biomass) and quality (i.e., body size) directly affect consumer fitness, but the effects of these factors are rarely measured in phenological studies. Moreover, energetic demand changes throughout an individual's life (Yang and Rudolf 2010), meaning that an individual's sensitivity to resource availability is not constant but is instead likely age-structured (Dunn et al. 2011). Viewing mismatching simply as asynchrony in time, instead of as the disrupted interaction between consumer demand and resource availability, can therefore obscure the cumulative effects of mismatching and mask population-level consequences (Yang and Rudolf 2010, Kerby et al. 2012). Although many conceptual models have been proposed to address this issue, a more robust methodology to model mismatching as the interaction of dynamic consumer demands and resources is still lacking (Chmura et al. 2019, Visser and Gienapp 2019).

Incorporating both age-structured consumer demand and multiple facets of resource availability into mismatch models likely requires a re-examination of our statistical concept of mismatching (Visser and Both 2005, Kellermann and van Riper 2015). Phenologies are generally modelled as frequency curves on a temporal axis (Fig. 3.1; Cushing, 1974, Visser et al. 1998), whereby a population's degree of match with their resource is estimated as the difference in peak dates (i.e., date models) or proportion of overlapping area (i.e., overlap models). Date models have been frequently criticized in the literature, however (Lindén 2018, Ramakers et al., 2020). While date and overlap models agree if consumer and resource curves are symmetrical (Fig. 3.1a,b), date models can be biased when phenologies are skewed or multimodal, or in cases of low resource availability (Fig. 3.1c,d,e). Because overlap models account for the full interaction of consumer demand and resource availability posed in the match-mismatch hypothesis (Kerby et al. 2012), they may be better able to capture the mechanism of mismatching.

Overlap models have performed inconsistently as well. This inconsistency may result from an inaccurate representation of consumer demand (Yang and Rudolf 2010, Kerby et al. 2012, Lindén 2018). Existing 'peak demand' overlap models estimate consumer demand from a single life-history event or timepoint in development, such as when individual growth rates are maximized (Fig. 3.2a; Leung et al. 2018). This approach, however, ignores demand prior to or following this peak, and results in a less realistic demand curve (Fig. 3.2b; Kerby et al., 2012, Lindén 2018). Because animals require increasing energy as they develop, their sensitivity to the low resource availability associated with mismatching is likely to change over time. As a result, measuring the consequences of a mismatch from one timepoint could shroud cumulative effects (Yang

and Rudolf 2010) and mask variation among individuals of differing ages (Reed et al. 2013). The growing availability of metabolic data and advances in survival analyses modeled in a Bayesian framework now allow for the direct simulation of the age- or stage-specific effects of mismatching. By modeling cumulative consumer demand as a function of the population age-structure, a 'whole demand' model incorporates the increasing metabolic demands of individuals as they age (Fig. 3.2c). As a result, the whole demand curve quantifies overlap at the demand curve's upper tail when per-capita consumer demands are likely greatest (Fig. 3.2d; Kerby et al. 2012). Accurately modeling consumer demand and competing factors of resource availability may therefore be key to defining how mismatching occurs and when it should matter to populations.

Migratory birds provide a powerful avenue to re-examine the effects of mismatches under this framework. Long-distance migrants represent some of the canonical examples of mismatches because of their use of endogenous cues to time migrations and reproduction (Both and Visser 2001), and their reliance on seasonal resource pulses to achieve rapid offspring growth (Schekkerman and Visser 2001). While many studies have identified individual-level fitness effects resulting from mismatches, few have found corresponding population-level consequences (Visser and Both 2005, Dunn et al. 2011). Hudsonian Godwits (*Limosa haemastica*; hereafter, 'godwits') are a case-in-point. Godwits breed in three disjunct populations spread across the Nearctic (Walker et al. 2011). Like other shorebird species (Kwon et al. 2019), godwits breeding in Alaska have kept pace with recent phenological changes in peak resource availability while those breeding in Hudson Bay have not (Senner 2012). Despite mismatches affecting the survival of individual godwit chicks in Hudson Bay, there have been few

apparent population-level consequences (Senner et al. 2017). Furthermore, much of the interannual variation in the fledging rates of Alaskan godwits is not explained by predation or density-dependent processes (Senner et al. 2017, Swift et al. 2017a, 2018, Wilde 2021b). The observed interannual variation may instead result from a potential correlation between early snowmelt and low annual godwit fledging rates, suggesting that mismatching may be occurring and having demographic consequences (Saalfeld et al. 2019).

Updating our conceptualization of mismatches may document the effects of resource availability on godwit fitness that our previous attempts based on the categorical view of mismatching have missed. Therefore, we investigated how dynamic consumer demand and resource characteristics interact to influence the potential for mismatching in the Alaskan population of godwits. We developed mechanistic models that integrate metabolic and resource availability information at the individual- and population-levels. We first explored how the timing, abundance, and quality of resources have changed over the course of the breeding season. Then, we investigated the effects of invertebrate abundance and size on the growth and survival of godwit chicks. We hypothesized that mismatching affects individual fitness differently throughout development and predicted that chick growth and survival would improve with more abundant and larger prey, with the effect of invertebrate body size increasing with age. Lastly, we investigated the influence mismatching has on godwit population dynamics. We hypothesized that mismatching in godwits is simultaneously a function of both consumer demand and resources. We therefore predicted that the whole demand model would explain population-level effects better than alternatives. Identifying how resources interact with

consumer demands will provide evidence for the mechanism underlying mismatches and help better connect mismatching to demographic processes.

Methods:

Study area and godwit chick monitoring

During 2009–2011, 2014–2016, and 2019, we monitored godwits on two plots – North (550 Ha) and South (120 Ha) – near Beluga River, Alaska (61.21°N, 151.03°W; hereafter, 'Beluga'; Appendix B: Fig. B.1). Both plots consist of freshwater ponds and black spruce (*Picea mariana*) outcroppings dominated by dwarf shrub and graminoids surrounded by boreal forest (Swift et al. 2017a, 2017b).

Each year (early-May to mid-July: $\bar{x}$ = 78 days), we censused both plots for godwit nests, locating, on average, 23 nests per year (range: 11–33). For each nest, we estimated hatch date by floating the eggs to estimate the age of the nest (Liebezeit et al. 2007). We monitored the nests' survival every 2–3 days until eggs showed starring or pipping, after which, we monitored them daily until hatch. We captured newly hatched chicks and collected morphometric measurements and body weights on all chicks in the brood. We uniquely marked each with a leg-flag and U.S. Geological Survey metal band, neither of which are likely to impact survival (Sharpe et al. 2009). Some nests hatched before detection each year (range: 0–4). We opportunistically captured chicks from these broods off-nest and estimated their age from weight measurements. Because we included chicks captured off-nest, we are confident that we found all broods each year given the small size of the study area and the conspicuousness of godwit broods.

We monitored the survival of 1–2 chicks chosen randomly from each brood (range = 7–23 chicks per year), except for one brood in 2019 from which we captured

two chicks >14 days after their estimated hatch date. We attached a 0.62 g very high frequency radio transmitter (Holohil Systems Ltd.) above the uropygial gland by clipping the feathers and using skin-safe, cyanoacrylate glue to attach the radios directly to the skin. We relocated each radioed chick every 2–3 days by walking the entirety of the study plot and recording telemetry azimuths from within <100 m of the tending parent(s)'s location. When no parents were present, we scanned for signals in all directions from a chick's last known location. We attempted to recapture radioed chicks weekly to reapply glue and measure their body mass to the nearest gram, minus the transmitter weight, using a magnetic field scale.

Godwits are fully flight capable, or 'fledged', after ~28 days (Walker et al. 2011). However, because our radios had an expected lifespan of 21-days (range: 17–30 d; Holohil Systems, 2021), we considered chicks that survived to 21 days to have fledged. We confirmed mortalities when possible and assumed that chicks had died after three consecutive failed relocation attempts. While it is possible that some radios failed, we did not record any instances in which this occurred and are confident that the lifespan of our radios was sufficient for capturing survival for two reasons: first, the chicks that died during monitoring did so on average by 3.6 days of age (SD: 8.3; range: 0–16), and second, we never resighted a chick that was presumed dead during weekly censuses of the bog and nearby foraging areas (N.R. Senner, University of South Carolina, unpublished data, 2019).

Resource monitoring

During 2009–2012, 2014–2017, and 2019, we monitored the abundance and body size of invertebrates. In 2009–2011, 2014–2016, and 2019, we monitored invertebrates for an

average of 67 days (range = 61–78) simultaneous with our godwit monitoring. Additionally, we monitored invertebrates, but not godwit nests, for 38 and 5 days in 2012 and 2017, respectively, as these were shortened seasons with limited crews. Passive traps are a good proxy of resource availability to foraging shorebird chicks (McKinnon et al. 2012). We thus collected invertebrates each day along two, 50-m transects consisting of five traps placed within mesic godwit breeding habitat (Brown et al. 2014, Senner et al. 2017). We used two trap styles: pitfall traps (10 × 15 cm) filled with 10 cm of 75% ethanol from 2009–2012, and modified malaise traps (see Leung et al. 2018) filled with 3 cm of 75% ethanol from 2014–2019. We cleared and replenished traps every 24 hours.

We identified invertebrates to Order and measured body-lengths to the nearest 0.5-mm. We converted lengths to dry mass using published, taxon specific length-weight relationships (Ganihar 1997, Rogers et al. 1977).

Statistical Analyses

Interannual resource variation

To examine resource availability over the course of our study, we investigated how the (1) date of peak abundance, (2) daily biomass (transect^{-1} day^{-1}; dry mass, mg), and (3) daily median invertebrate body size (per-capita dry mass, mg) changed across years. Because godwit chicks are gape limited and rarely consume larval invertebrates, we restricted our analysis to only include individual invertebrates that are potential prey for godwits by subsetting our data to include only adult invertebrates with lengths of 1.5–9 mm (Schekkerman and Boele 2009). We also excluded the shortened 2012 and 2017 seasons from our analyses of the timing of annual peak abundance but included them in tests of daily biomass and daily median body size. We treated the transects as replicates,

averaging the total daily biomass collected along each transect for each day. We then estimated overall and order-specific annual peaks using the first derivative of quadratic curves (Julian day + Julian day^2) fit to the daily biomass within each year. We built separate mixed-effect models to estimate linear trends over time in the overall and order-specific dates of peak abundance (i.e., peak dates), daily biomass, and daily median body size. We included a random intercept for 'trap type' in all our models using the *lmer* function (package 'lme4', Bates et al. 2015) in the R programming environment (v4.0.3, R Core Team 2020). In the daily biomass and daily median invertebrate body size models, we also included a random intercept of sample date to compare trends within days of the year over the course of the study.

To identify potential changes in the composition of the invertebrate assemblage, we repeated the above analyses with each of the six Orders that comprised 91.6% of all observed invertebrates – Araneae (20.5%), Hymenoptera (18.4%), Coleoptera (17.5%), Diptera (16.2%), Acari (11.3%), and Hemiptera (7.7%; Appendix B: Fig. B.2). We excluded Collembola (8.3%) from our analyses, as they are primarily aquatic and thus unlikely prey for godwit chicks and were also poorly recorded, due to their low frequency from 2009–2012. We standardized response variables by dividing by two standard deviation according to Gelman (2008), but report coefficients in their original units throughout the text. We considered response variables whose 95% confidence intervals did not include zero as biologically relevant.

Chick growth and body condition

We modelled chick growth with a logistic growth function using the 'nlme' package (Pinheiro et al. 2020) to predict the age-specific mass of chicks (Senner et al. 2017).

Although godwit chicks may be sexually dimorphic (Loonstra et al. 2018), we lacked data on each individual's sex and therefore pooled the sexes in our analyses. We set the asymptotic mass to the population's mean adult mass (249 g; Senner et al. 2017). Next, we developed separate growth models with chick ID as a random intercept, and constant or annual growth coefficients and inflection points (Pinheiro and Bates 2000). We performed 100 iterations for each model and included site-specific estimates from Senner et al. (2017) as starting values. We compared 12 candidate models using Akaike's Information Criterion scores corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). We used candidate models with <2 ΔAIC_c to estimate the predicted chick growth curve. Next, we calculated the body condition index (BCI) for each recaptured individual by dividing the observed weight gain since last capture by the curve-predicted weight gain over the same time.

To investigate whether and over what timescale resource characteristics influenced chick growth, we modelled BCI in relation to resource abundance and quality in all years with godwit monitoring except 2014, which lacked sufficient chick recaptures. We built a global, generalized additive mixed model (GAMM) with a gaussian error term that included (1) daily invertebrate biomass, (2) daily median invertebrate body size, and (3) hatch date as fixed effects (package 'gamlss'; Rigby and Stasinopoulos 2005). We included random intercepts for (4) year and (5) brood ID. Lastly, we (6) smoothed the effect of chick age using a cubic spline to account for irregular sampling (every 7-days) throughout development. We first ensured that all additive covariates included in the same model showed minimal collinearity with a pairwise Pearson's correlation coefficient (r) below 0.7 (Appendix B: Table B.1).

Because resource abundance and quality could have either an immediate or cumulative effect, we determined the timescale over which these predictors influenced BCI: day of recapture or 1-day, 3-day, or 7-day averages, and used the timescale with the lowest AIC_c score in further analyses. We also determined whether including random intercepts – individual, brood, or year – improved model fit with an AIC_c comparison. Finally, we built a global model with the timescale and random effects that optimized fit and compared all candidate models using AIC_c scores. When no model had a model weight (w_i) > 0.90, we used model averaging ($\Delta AIC_c < 4$) within the 'MuMIn' package and report conditional average coefficients (Bartoń 2015).

Effect of resources on survival: constant or age-varying?

To determine how invertebrate biomass or body size affected daily chick survival, we built a Bayesian hierarchical survival model. We constructed daily encounter histories for all individuals, beginning with an individual's hatch date and ending with their expected fledging date. Because we assumed the chicks that we could not relocate for three consecutive days were dead, we included two days of unknown fate to allow for Markov chain Monte Carlo (MCMC) prediction. We modelled encounter histories as a Bernoulli variable and assumed fates were known.

In the second portion of our model, we incorporated parameters hypothesized to influence chick survival. We constructed a logit-linear mixed model to estimate the additive effects of (1) daily invertebrate biomass, (2) daily median invertebrate body size, (3) hatch date, and (4) chick age, along with random intercepts for each (5) brood ID, (6) year, and (7) study plot. To reduce the influence of outlier values of daily biomass or daily median size measurements, we averaged our continuous parameters across 3-day

periods (i.e., our relocation interval) and standardized all variables by dividing by two standard deviations (Gelman 2008). To test whether the effects of daily invertebrate body size or daily biomass varied with chick age, we built separate models with interactive terms between chick age and either daily median invertebrate body size or daily invertebrate biomass. Given their rapid growth rates, age is a proxy for mass-specific resting metabolic rates in shorebird chicks (Schekkerman and Visser 2001, Williams et al. 2007). The Pearson's correlation coefficient (r) between age and godwit mass used to calculate mass-specific resting metabolic rate from Williams et al. (2007) was 0.84. Therefore, we used age as a proxy for resting metabolic rate given the lack of high-resolution mass measurements. We compared these age-interaction models using deviance information criterion (DIC) and included the interaction from the model with the lower DIC score in all further models. We chose diffuse priors for all our predictors (Normal(0, τ)) and constrained random intercepts close to 0 (mean = N(0, 1000), SD = Uniform(0, 25)).

To identify the top model, we performed model selection using the indicator-variable approach (Link and Barker 2006, Converse et al. 2013). We again checked for collinearity between additive covariates with a pairwise Pearson's correlation coefficient (Appendix B: Table B.2). Next, we assigned a Bernoulli variable (weights) with a 0.5 prior to each predictor to model its inclusion (1) or absence (0) from each MCMC sample. We maintained an equal number of parameters across samples by fixing the model variance, $\tau = K * \text{Gamma}(3.29, 7.8)$, for all parameters, where K is the number of parameters (Link and Barker 2006). The posterior mean of the weight indicator is evidence for inclusion in the model. We calculated Bayes factors (BF) from predictor

weights (Link and Barker 2006) and included predictors with BF > 3 in our top model along with their random intercepts. If an interaction term was selected for the top model, we included both additive terms included in the interaction regardless of their independent selection.

We constructed models of daily chick survival using the 'runjags' and 'rjags' packages (JAGS 4.1.0; Plummer 2012, 2013, Denwood, 2016). Our models accessed three parallel chains to perform 5,000 iterations. We removed 600 and 1,000 iterations for adaptation and burn-in, respectively, with a one-third thinning factor. We assessed model performance based on the values of the Gelman-Rubin statistic < 1.1 and chain mixing (Gelman and Rubin 1992). For all tests, we report the beta coefficients in logit-form, 95% credible interval, and Bayesian p-value (probability of slope ≠ 0).

Population match and reproductive success

To quantify population-level mismatching, we built resource and consumer demand curves for each year. Additionally, we built competing demand curves from the 'peak demand' and 'whole demand' conceptual models (Fig. 3.2) to quantify the effect of dynamic consumer demand on godwit reproductive success. (1) *Peak demand*: Following Kwon et al. (2019), we calculated the number of all hatched godwit chicks expected to be 11-days old (i.e., age of peak growth rate; Senner et al. 2017) for each day of the season. We then converted both the daily values of invertebrate biomass (hereafter, 'resource curve') and counts of 11-day old chicks to their annual proportions. (2) *Whole demand*: We estimated the cumulative mass of all chicks per day of the pre-fledge period in each year from our growth curve and used this to calculate daily estimates of mass-specific resting metabolic rate in godwit chicks (Williams et al. 2007). Resting metabolic rate

approximates the amount of energy individuals use to maintain homeostasis and therefore represents an individual's minimum energetic requirement independent of other factors (i.e., thermal environment). We then estimated the cumulative energetic requirements (Kilojoules d^{-1}) of all chicks per day of the season and converted these to annual proportions to produce the whole demand curve.

We modelled the shape of the peak demand, whole demand, and resource curves using separate GAMs with a quadratic time function – Julian day + Julian day^2 (Kwon et al. 2019). We restricted the analyses to 10 May – 10 July for comparison among years, which otherwise differed in length (Appendix B: Table B.3). We approximated error terms as a gaussian distribution (~N[μ,σ]) and zero-inflated beta distributions (~ zBeta[z|α, β]) for the peak demand and whole demand curves, respectively, and a beta distribution (~Beta[α, β]) for the resource curve, all with logit-link functions. We fit the resource curve with a penalized spline (k = 10) to estimate mean predicted values for each day of the season while capturing the modality of the resource curve (Vatka et al. 2016). We then estimated the degree of overlap between the peak demand or whole demand curves and the resource curve by calculating the proportional area overlap using the *integrate.xy* function ('sfsmisc', Maechler 2020). We also estimated (3) the 'difference in peak dates' (i.e., synchrony) between the resource and peak demand curves in each year from the point at which each curve's derivative was zero and the (4) 'curve height' in each year (i.e., cumulative resource availability) from the area under the resource curve.

To determine how mismatching affected godwit reproductive success, we built four univariate linear models relating the different measures of mismatching to fledging

rates – (1) peak demand, (2) whole demand, (3) difference in peak dates, and (4) curve height. We extrapolated daily survival rate estimates from our global Bayesian model to 28 days with the associated error using the Delta method (Powell 2007). We compared among the four models by calculating model weights from their AIC_c scores and the proportion of the variation in fledging rates they explained.

Results:

We located 142 godwit nests from 2009–2019, of which 128 survived to hatch. We individually marked 349 chicks (2009–2011, *n* = 195; 2014–2016, *n* = 106; 2019, *n* = 48) and attached radios to 128 chicks from 102 distinct broods. On average, radioed chicks survived to 9.4 days (SD: 8.4 d, range: 0–21). We relocated radioed chicks an average of 4.3 times (SD = 2.71, range: 1–19; *n* = 778), and we recaptured them 1.5 times (SD: 0.83; *n* = 103). In most cases of chick death, we located a carcass (38%) or found a detached radio in habitats clearly suggestive of predators (20%; e.g., on gull nesting island) within 2 days (range: 0–4 days) of the first failed relocation attempt.

Interannual resource variation

We recorded the body-lengths of 69,598 adult invertebrates across 14 orders, 41,298 of which were potential godwit prey (i.e., 1.5–9 mm in length) and thus considered in our analyses. Sample days showed wide variation in the biomass ($\overline{x}$ = 132.9 mg, range: 0–948.4 mg) and daily median body size ($\overline{x}$ = 1.5 mg, range: 0.2–13.4 mg). We found no change in the timing of the predicted peak dates of all invertebrates (β = -1.68 ± 3.08 d, 95% CI = -3.34, 5.50 d; R^2_m = -0.02; R^2_c = -0.05) or among the individual orders over the course of the study (Fig. 3.3, left). However, both daily invertebrate biomass (β = -2.49 ± 0.50 mg, 95% CI = -3.49, -1.51; R^2_m = -0.18; R^2_c = -0.35; Fig. 3.3, center) and daily

median invertebrate body size (β = -0.33 ± 0.03 mg, 95% CI = -0.028, -0.37; R^2_m = -0.13; R^2_c = -0.26; Fig. 3.3, right) did decrease over time at a rate of -2% and -5% per year, respectively. At the Order level, only Acari became more abundant over time (β = 0.20 ± 0.02 mg, 95% CI = 0.15, 0.25; R^2_m = 0.14; R^2_c = 0.38), while all other taxa became less abundant. Additionally, Araneae (β = -0.67 ± 0.09 mg, 95% CI = -0.49,-0.85; R^2_m = -0.19; R^2_c = -0.28), Diptera (β = -0.24 ± 0.02 mg, 95% CI = -0.20, -0.29; R^2_m = -0.03; R^2_c = -0.15), and Hemiptera (β = -0.23 ± 0.06 mg, 95% CI = -0.10, -0.35; R^2_m = -0.11; R^2_c = -0.16) showed consistent decreases in body size over the course of the study.

We found opposing trends in daily biomass during the early and late portions of the godwit breeding season. Days during the nest incubation period (16 May–6 Jun) from 2014–2019 had 83% higher invertebrate biomass than those from 2009–2012, but 41% lower biomass on days during the chick-rearing period (6 Jun – 4 Jul). Meanwhile, invertebrate body size was 42–72% smaller in the later period.

Chick growth and body condition

We modeled godwit chick growth from 103 mass-at-capture measurements taken following the initial measures collected at hatch. We estimated a predicted growth curve only from our top model as the next best model had a $\Delta AIC_c > 6$ (Appendix B: Table B.4). Chick growth did not differ among years, and our top-performing growth function included both a constant logistic coefficient ($K = 0.13 \pm 4.2\times10^{-3}$) and inflection point ($T_i$ = 17.5 ± 0.5 days).

The fit of our global model was greatest using 7-day averages of our continuous variables – daily biomass and daily median body size – and no random effects (Appendix B: Table B.5). Our top model explaining chick BCI (*n* = 89) included invertebrate

biomass and hatch date with a smoothed age effect (w_i = 0.75; Appendix B: Table B.6). Chick growth improved with higher invertebrate biomass ($\beta = 1.8 \times 10^{-4} \pm 3.8 \times 10^{-5}$ mg^{-1}, CI = 1.2×10^{-4}, 2.8×10^{-4}; $R^2_{adj.} = 0.37$; Fig. 3.4a) but decreased with later hatch dates ($\beta = -0.013 \pm 0.003$ d^{-1}, CI = -0.0053, -0.019; Fig. 3.4b). Invertebrate body size had no consistent effect (Appendix B: Fig. B.3). Chicks had 3–75% higher body condition indices during periods with higher-than-average invertebrate biomass compared to periods with low invertebrate abundance. In terms of phenology, chicks grew better than expected if they hatched before 5 Jun but worse than expected if they hatched after that date.

Effect of resources on survival: constant or age-varying?

Of the 128 godwit chicks in our study, we excluded 6 due to human-caused mortality or instances when the radio fell off on the day of deployment. The mean DSR of the remaining 122 chicks was 86 ± 24%, meaning that 19.2 ± 33% survived to fledge, although this varied among years and broods (Appendix B: Table B.7).

The model with an age-varying effect of invertebrate body size (DIC = 282.2) outperformed the model with an age-varying effect of invertebrate biomass (DIC = 288.7). We therefore used the former in our subsequent models. The constant effect of invertebrate biomass and the age-varying invertebrate size effect had 79% and 85% posterior inclusion probabilities, respectively (Table 3.1). We also included constant effects of age and invertebrate size to accompany the interaction term.

Chick survival improved with greater invertebrate biomass and larger invertebrate body sizes, and the latter effect increased throughout development (Table 3.2). Each 1% increase in daily invertebrate biomass (+ 1.5 mg) improved daily chick survival by 0.66%

(Fig. 3.5a), while each 1% increase in median invertebrate body size (+ 0.06 mg) led to a 1.02% increase in daily chick survival. This 'size' effect then grew by 2.2% with each day that a chick survived (Fig. 3.5b). Age itself, however, had no consistent effect on chick survival. Daily chick survival was, on average, 17% higher during periods of above average invertebrate biomass, and 29% higher in these instances for chicks below 5-days of age and 50–72% higher for chicks 11–21 d.

Population match and reproductive success

The model fit for the whole demand curve (AIC_c = -300.1) was 25.7-times better than the peak demand curve (AIC_c = –248.7). Godwits had, on average, 51.9 ± 9.2% overlap with resource phenology according to the peak demand model, but 44.7 ± 11.6% overlap according to the whole demand model. Years also differed in curve height ($\overline{x}$ = 8,800 ± 3,668 mg) and the difference between the peak dates of the resource and demand curves ($\overline{x}$ = 14.7 ± 16.36 d; Appendix B: Fig. B.4, B.5).

Godwit fledging rates did not decrease linearly through time (Appendix B: Table B.8) but were lowest in 2014 and 2015. Those years had ~19% poorer overlap and ~28 days greater mismatching compared to the long-term average. Mismatching on this scale resulted in 24% lower fledging rates and near complete reproductive failure for the population. Models differed in their ability to explain population-level reproductive success but the whole demand model was best supported (Appendix B: Table B.9). The whole demand model explained 55% of the variation in godwit fledging rates (β = 1.19 ± 0.41; $R^2_{adj.}$ = 0.55; w_i = 0.43; Fig. 3.6 upper left; Appendix B: Fig. B.4). The 'difference in peak dates' model performed similarly well (β = -0.68 ± 0.27; $R^2_{adj.}$ = 0.48; w_i = 0.36; Fig. 3.6 upper left) but was 7% less likely to be the top model. Both the peak demand

overlap ($\beta = 1.00 \pm 0.56$; $R^2_{adj.} = 0.26$; $w_i = 0.11$; Fig. 3.6 lower left; Appendix B: Fig. B.5) and curve height models ($\beta = 2.49 \pm 1.44$; $R^2_{adj.} = 0.25$; $w_i = 0.10$; Fig. 3.6 lower right) were unlikely to be the top model given their low model weights and the low amounts of interannual variation in fledging rates explained by either.

Discussion:

The disconnect between empirical results and the theoretical predictions of the match-mismatch hypothesis make it difficult to assess the effects of climate change-induced phenological mismatches on consumer populations (Visser and Gienapp 2019, Keogan et al. 2020). To remedy this gap and connect mismatches to demographic processes, Kharouba and Wolkovich (2020) urged researchers to define pre-climate change baselines, collect per-capita data on resources and consumers, and test competing biological mechanisms. We developed mismatch models aimed at fulfilling these recommendations while adopting an age-structured representation of consumer demand. Using this approach, we built upon the findings of Senner et al. (2017) and identified heretofore undetected individual- and population-level fitness effects of mismatching in the Alaskan breeding population of Hudsonian godwits. Our study joins the growing literature suggesting that mismatches do not fall neatly into a 'matched' or 'mismatched' paradigm (Keogan et al. 2020, Simmonds et al. 2020). Instead, models built around the underlying biological mechanisms connecting consumers and resources are key to clarifying how mismatching affects consumer fitness (Takimoto and Sato 2020).

More than mistiming: the tandem drivers of resource availability

We found that resources affected godwit chick survival in two distinct ways: first, periods with reduced resource abundance resulted in poorer growth and lower survival and,

second, access to larger invertebrates was increasingly important to the survival of older chicks. Our findings differ from those of previous godwit studies, which found no effects of limited resource availability in the Alaskan godwit breeding population (Senner et al. 2017). While these studies did not investigate the influence of invertebrate body size on godwit chicks, our contradictory conclusions likely stem from our use of hierarchical models that can approximate time-varying effects on survival (Royle and Dorazio 2009). Increasing energetic demands throughout ontogeny means that the effects of resource limitation are unlikely to be constant over an individual's lifetime (Yang and Rudolf 2010, Takimoto and Sato 2020). Therefore, models that accommodate varying predictor effects may be key to clarifying how resource characteristics affect consumer fitness.

Godwit chicks had improved growth and survival following periods with high resource abundance. Having adequate resources during energetically demanding periods is a primary driver of animal fitness (Bastille-Rousseau et al. 2015), especially in highly seasonal environments (McKinnon et al. 2012). Given their high energetic demands and rapid development, chicks of shorebird species across the Arctic exhibit survival costs following reduced resource abundance (Schekkerman et al. 2003, Saalfeld et al. 2019). Accordingly, godwit chicks in this study had higher body condition indices and higher daily survival probabilities during periods of higher-than-average invertebrate abundance. While we also detected effects of hatch date (i.e., phenology) on chick growth, these did not translate into an effect on survival. Our results therefore suggest that relating fitness measures to resource availability captures the effects of mismatching while defining its specific costs in biological terms (Dunn et al. 2011).

In addition to the effects of resource abundance, the quality (i.e., daily median body size) of invertebrates became increasingly important as godwit chicks aged. Optimal foraging theory predicts that consumers should select resources with the most energy content relative to foraging effort (Krebs et al. 1977). Chicks of black-tailed godwits (*Limosa limosa*), for instance, prioritize the rapid intake of small prey early in life, but switch to the slower intake of larger prey as they grow older (Schekkerman and Boele 2009). While we did not observe foraging behaviors directly, we hypothesize that Hudsonian godwit chicks may make a similar transition and increasing selection for larger prey could explain the especially high costs of poor resource quality for older chicks we found. Changes in resource quality, though rarely explored in the context of mismatches, can enact strong selection on consumer populations (Keogan et al. 2020, Yang et al. 2020). Because some individuals will encounter high-quality conditions in years when they are 'mismatched' (Kerby et al. 2012), accounting for the effects of multiple aspects of resource availability could improve our ability to document the true effects of mismatching.

Taken together, the additive effects of resource quantity and quality are likely to worsen in Beluga given the changes we observed in the invertebrate community. Climate-induced reductions in resource availability are common across terrestrial and marine systems (Bowden et al. 2015, Weterings et al. 2018). Arctic invertebrates, in particular, are simultaneously emerging earlier (Høye et al. 2007), becoming less abundant (van Klink et al. 2020), and smaller in size (Bowden et al. 2015, Jonsson et al. 2015) with increasing spring temperatures. Here, we found a linear decrease in the daily abundance and daily median body size of invertebrates, but no change in the date of peak

occurrence of invertebrates over the course of our study. Although we did not detect a change in the timing of the resource peak, we found opposing trends over time in the abundance of invertebrates during the early and late portions of the godwit breeding season. Therefore, should these trends continue, developing godwit chicks may face increasingly untenable conditions as food becomes both less abundant and poorer in quality (i.e., smaller size). More broadly, our results suggest that resource timing, quality, and quantity can act as concomitant drivers of phenological mismatches (Rollins and Benard 2020), and that their effects may be most apparent when placed in the context of the consumer life cycle (Yang et al. 2020).

Modeling the demand-resource interaction clarifies the population effects of mismatching

Variation in godwit reproductive success at the population level was best explained by our whole demand model of mismatches, although the simpler difference in dates model also performed well. Estimates from overlap and dates models often correlate (Ramakers et al. 2020), but may perform differently depending on a species' life history and degree of trophic specialization (Miller-Rushing et al. 2010). Thus, while difference in dates models may suffice for godwits and other species with narrow, synchronous breeding phenologies or those that rely on singular resource pulses (Miller-Rushing et al. 2010), they would likely perform poorly in species with highly variable nest initiation dates or those capable of multiple nesting events (Phillimore et al. 2016). Furthermore, difference in dates models could prove less accurate than whole demand models when resource phenology is multimodal or lacks a clearly defined peak, such as those typical of the temperate zone (Pearce-Higgins et al. 2005). Because overlap models account for both synchrony and the magnitude of available energy between interacting consumer-resource

pairs, they are more likely to capture mismatching as a disrupted interaction (Kerby et al. 2012). Overlap models are therefore likely more generalizable, but using both overlap and difference in dates models could help when exploring how mismatching occurs on a case-by-case basis (Kellermann and van Riper 2015).

Not all overlap models are equivalent, however. Overlap models have received mixed support (Ramakers et al. 2020), but their ability to accurately quantify mismatching at the tails of the consumer curve has been suggested as an important component of their effectiveness (Kerby et al. 2012). Whereas our peak demand model performed relatively poorly, our whole demand model explained the most variation in fledging rates among our suite of models. The difference between the two models' performance likely stems from the inability of the peak demand model to accurately capture consumer demand at the upper (i.e., right-hand) tail of the consumer curve, corresponding to the period when individual-level consumer demand is greatest. Our results therefore show that incorporating additional nuance into the statistical concept of consumer phenologies can greatly improve overlap models (Lindén 2018).

The need to accurately identify mismatches is made most clear by the accumulating evidence for variable and non-linear responses by consumer populations to mismatching (Visser and Both 2005, Phillimore et al. 2016). So called 'tipping points' – thresholds past which an effect abruptly changes (Latty and Dakos 2019) – buffer consumer populations from the negative impacts of moderate mismatching and may contribute to the lack of consistent responses to mismatching across consumer populations (Simmonds et al. 2020). In this population of godwits, we found that greater population-level mismatching consistently drove poorer fledging success, but that there

may be thresholds past which the effects are most severe. For instance, the degree of mismatch in 2014 and 2015 resulted in near complete reproductive failure for the population. Similarly low fledging rates for Hudson Bay breeding godwits, which are mismatched by 11-days on-average (Senner et al. 2017), suggests that for godwits, this tipping point may exist when populations are mismatched by more than ~10 days or have less than 40% overlap with the resource curve.

Importantly though, the 2014 and 2015 breeding seasons in Beluga coincided with a period of anomalous and prolonged near-surface warming in the northeastern Pacific called the 'blob' (Cavole et al. 2016). Thus, while the conditions in these atypical years may provide useful insights into potential outcomes of a warming climate on coastal communities in the region (Auth et al. 2018), mismatches of this magnitude are unlikely to become the norm. Beluga godwits have been able to advance their timing of migration and reproduction in response to recent long-term, linear warming trends (Senner 2012, Senner et al. 2017). Their ability to do so into the future will depend on whether the cues godwits use to time their annual cycle remain predictive of the timing of resource pulses on their breeding grounds. The significant spring warming and earlier snow disappearance dates projected for the North American sub-Arctic, for instance, means that godwits and other migratory populations may soon face accelerating, potentially non-linear warming to which they have limited capacity to respond (Love et al. 2010, Lader et al. 2020). Quantifying the strength and effects of mismatching in real time will thus be crucial for conservation going forward (Simmonds et al. 2020).

Conclusions

By modeling the unspoken assumptions of the match-mismatch hypothesis, we stand to adopt a more powerful definition of mismatching in biological terms and, in so doing, be better able to identify the circumstances under which consumer populations perform poorly. Our work also illustrates the role of ontogeny in shaping an individual's changing response to resource availability over time (Yang and Rudolf 2010), and helps explain the empirical-theoretical disconnect in phenological studies. Importantly, our models are transferrable to other systems, whereby remotely-sensed indices and knowledge of a population's age-structure could approximate resource availability and energetic requirements, respectively, when these data are otherwise unavailable (Lumbierres et al. 2017). Finally, we show how treating mismatches as an outcome of both consumer demand and resource dynamics provides insight into the structure of individual-level effects and the mechanism behind population-level responses (Takimoto and Sato 2020). Replacing the categorical 'matched' or 'mismatched' view of mismatching with one that explicitly recognizes the underlying mechanism may be critical to monitoring and conserving animal populations in an uncertain future.

Table 3.1. Bayesian model selection on variables in a global logistic model predicting daily survival rate in Hudsonian godwit chicks near Beluga River, AK from 2009–2019. Predictors were selected using the indicator-variable approach, in which posterior inclusion probabilities (weights) and Bayes Factors (BF) were estimated from a Bernoulli variable associated with each predictor. Variables of the global model with BF > 3 and their component parts (i.e., interaction terms) were included in the top model. Age: number of days since hatch; Hatch: individual's hatch date; Size: daily median invertebrate body size; Biomass: daily invertebrate biomass.

Variable	*Weight, global*	*BF, global*	*Weight, top*	*BF, top*
Age	0.53	1.125	0.52	1.081
Size	0.54	1.177	0.52	1.068
Hatch	0.54	1.175	-	-
Biomass	0.79	3.730	0.77	3.340
Age × Size	0.85	5.614	0.80	4.042

Table 3.2. Standardized effect of variables on the survival rates of Hudsonian godwit chicks near Beluga River, AK from 2009–2019. Posterior probabilities were estimated from a hierarchical model (n = 122, posterior samples = 5000) with both survival and stochastic model components. Age: number of days since hatch; Hatch: individual's hatch date; Size: daily median invertebrate body size; Biomass: daily invertebrate biomass.

Predictor	*Mean (SD)*	*95% Credible Interval*	*Pr ≠ 0*
Intercept	-2.388 (5.253)	-13.10, 7.17	0.35
Age	-0.001 (0.201)	-0.41, 0.38	0.48
Size	0.331 (0.185)	-0.03, 0.71	0.96
Biomass	0.26 (0.169)	-0.08, 0.58	0.87
Age × Size	0.679 (0.103)	0.48, 0.88	1.00

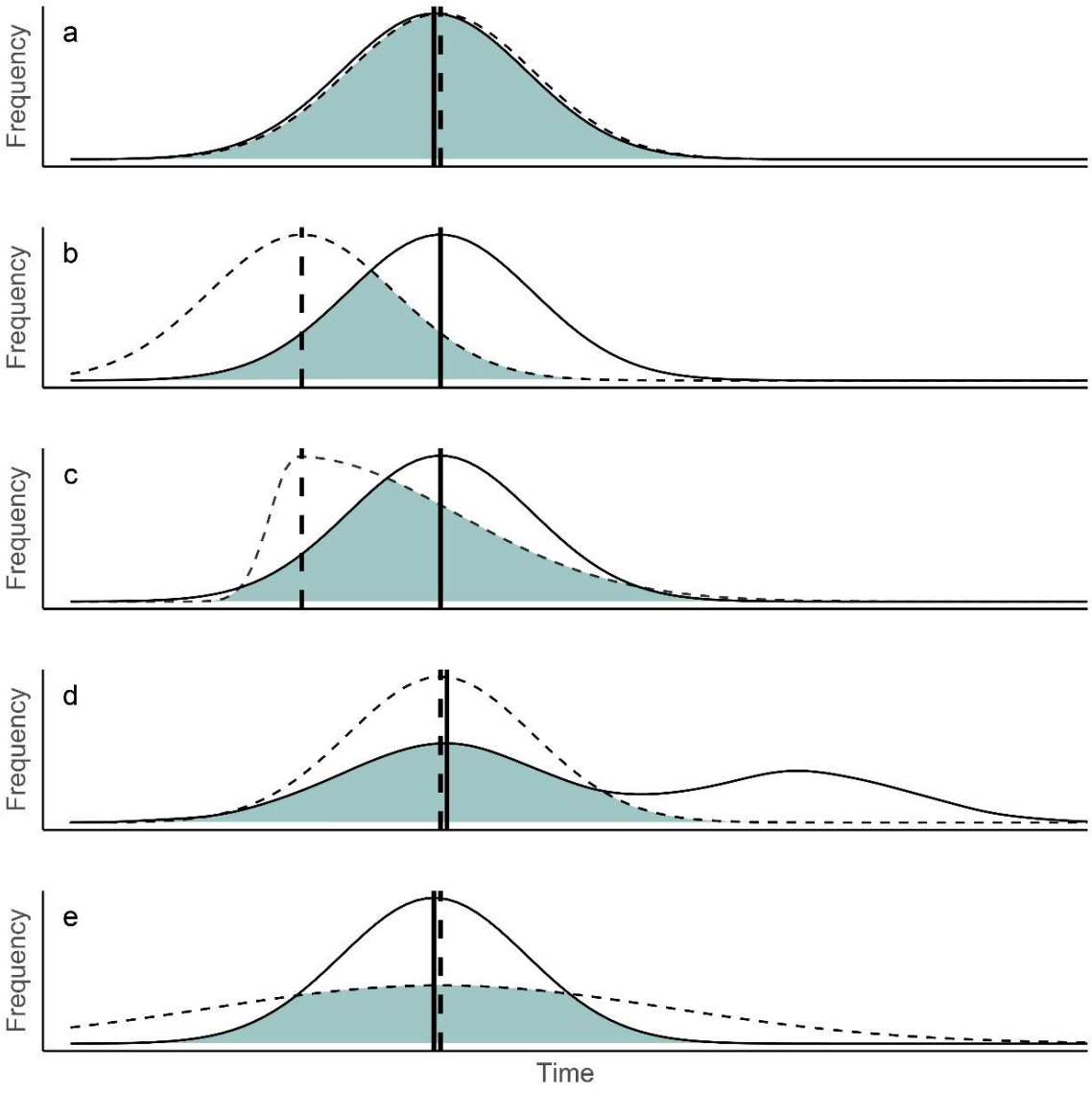

Figure 3.1. Peak dates (vertical lines) and frequency curves (phenologies) of consumers (solid) and resources (dashed). Difference in peak dates and peak overlap (shaded area; percent area under the curve) models are approximately equivalent when both the consumer (solid) and resource (dashed) curves are symmetrical (a, b). In this case (b), mismatching is a function of temporal displacement. However, date and overlap model estimates differ when either curve is skewed (c), the consumer phenology is multimodal (d), or the curves are aligned but have low overlapping area due to reduced resource abundance (e).

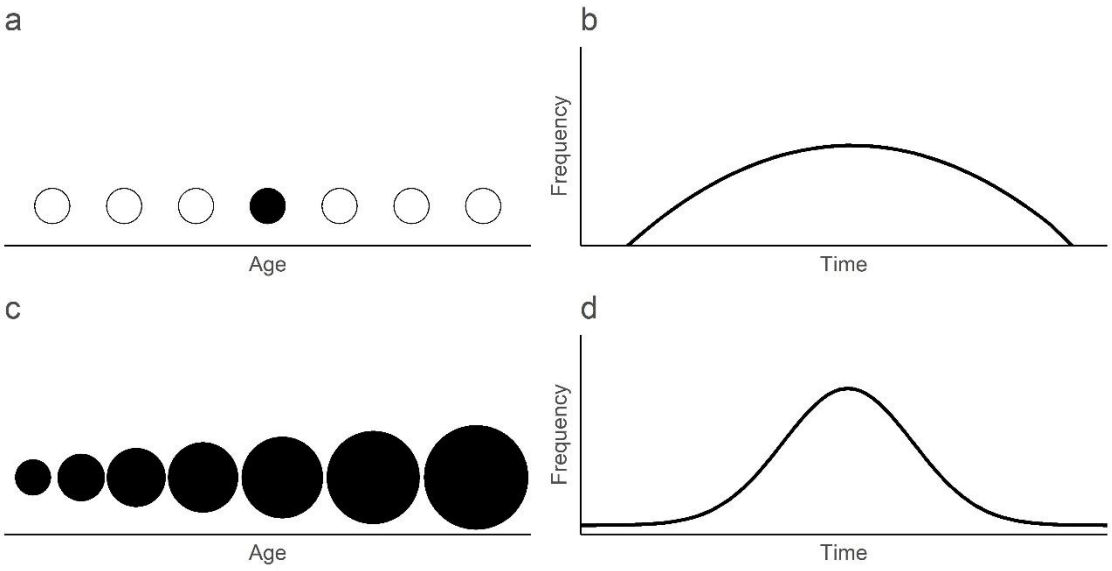

Figure 3.2. The peak demand model estimates consumer phenologies from the daily frequency of individuals at a single point in development (e.g., peak growth rate; a). Fitting a curve to pseudo-discrete data of this kind results in a simplified curve (b). However, since resource demand increases throughout development (c), including the cumulative demand of all individuals for each day of the season produces a curve with well-defined tails (d). Filled circles are time points in an individual's development considered by the model. Circle size corresponds with hypothetical energy requirements at each timepoint. Curves are from predictions from a generalized additive mixed model performed on data collected in our study (see Methods and Results).

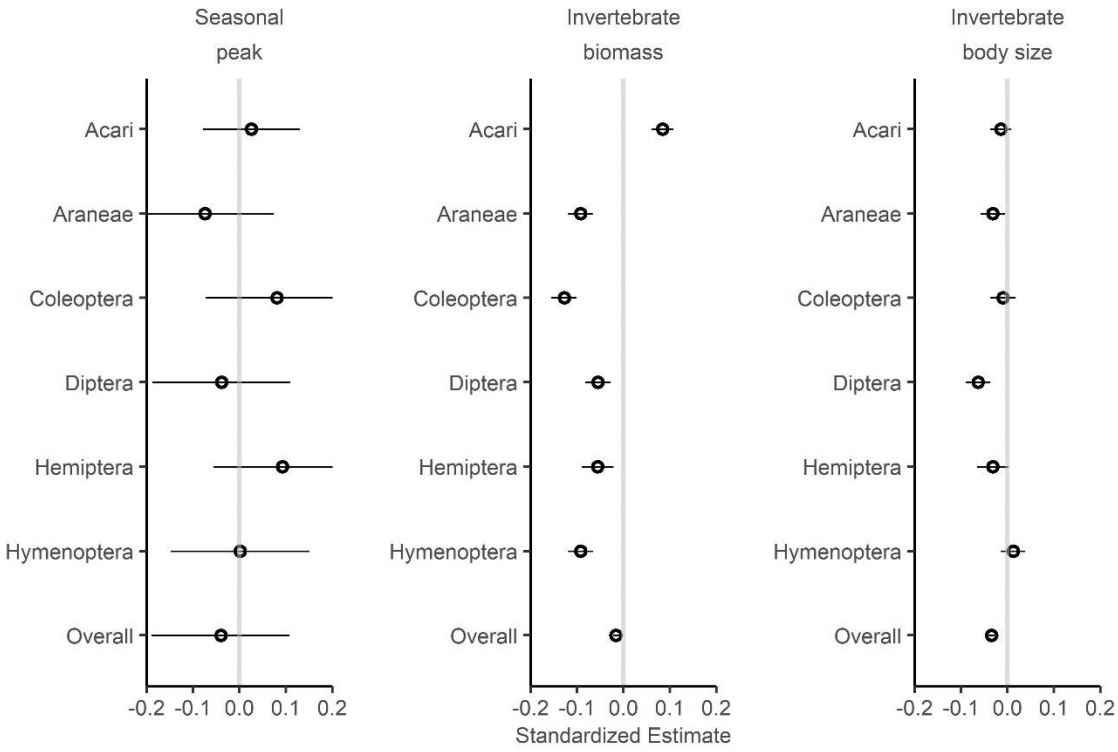

Figure 3.3. Interannual changes of the timing of peak abundance (left), observed daily invertebrate biomass (center), and daily median invertebrate body size (right) of six common Orders and the invertebrate assemblage overall. Linear regression estimates are shown as hollow circles, with 95% confidence intervals shown as horizontal lines. Variables with no consistent effect had intervals that crossed zero (grey line).

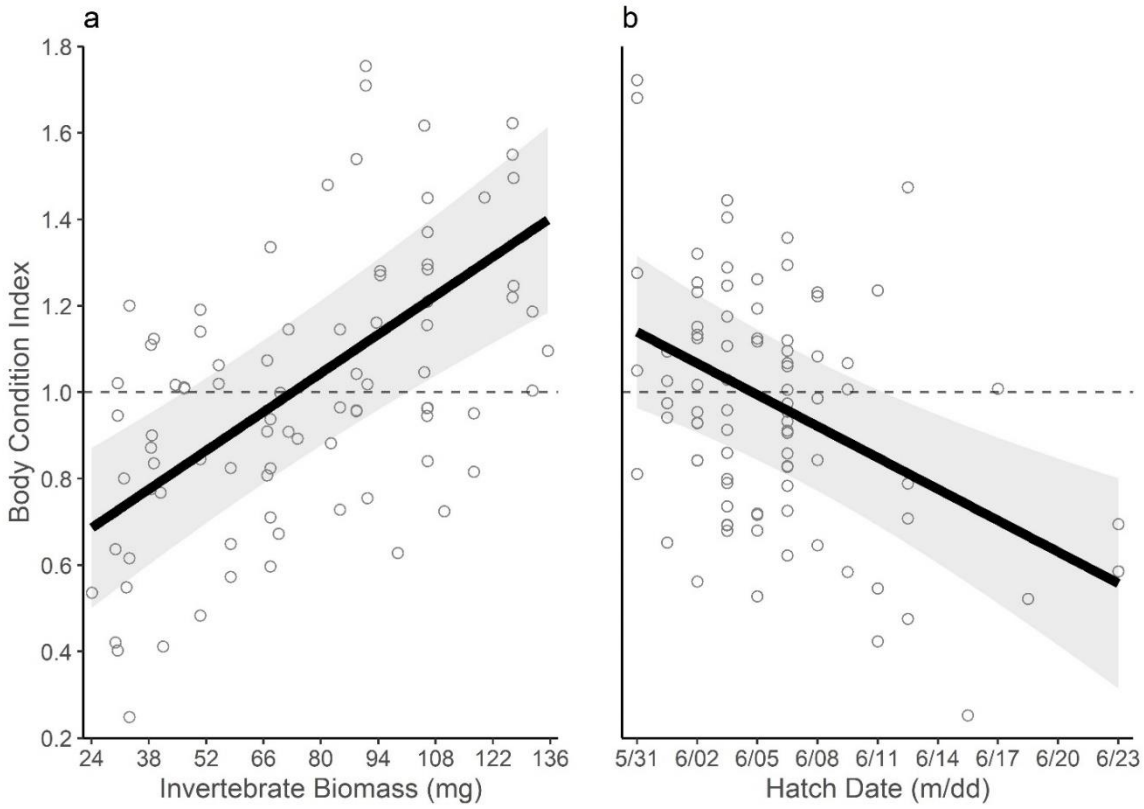

Figure 3.4. Effect of daily invertebrate biomass (a) and hatch date (b) on Hudsonian godwit chick body condition index (BCI). BCI (hollow points) is the ratio of the observed to expected weight gain since an individual's last measurement. BCI > 1 correspond with above average growth and BCI < 1 below average growth (dashed line). Regression line (black) and 95% confidence interval (grey) are shown.

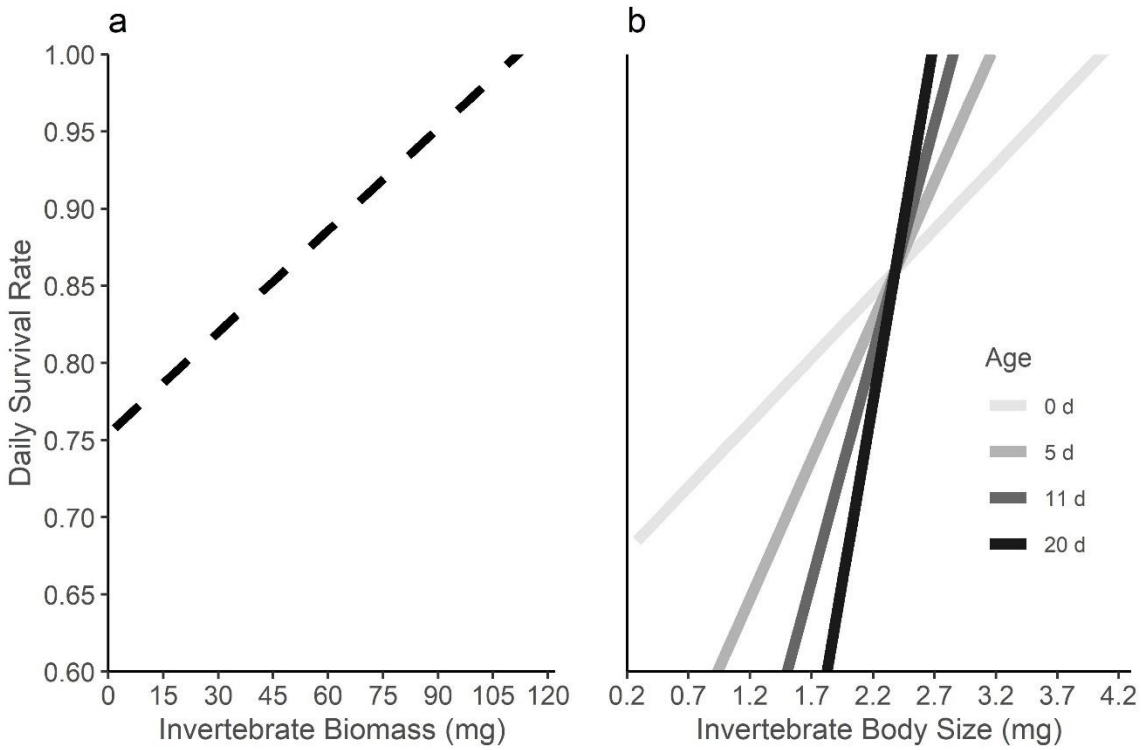

Figure 3.5. Effects of daily invertebrate biomass (a) and invertebrate body size (b) on the daily survival of Hudsonian godwit chicks from the posterior mean estimates of a Bayesian hierarchical model (credible intervals not shown). Biomass (a; dashed) had a constant effect, but the effect of size varied with age (b; shade of grey, in days).

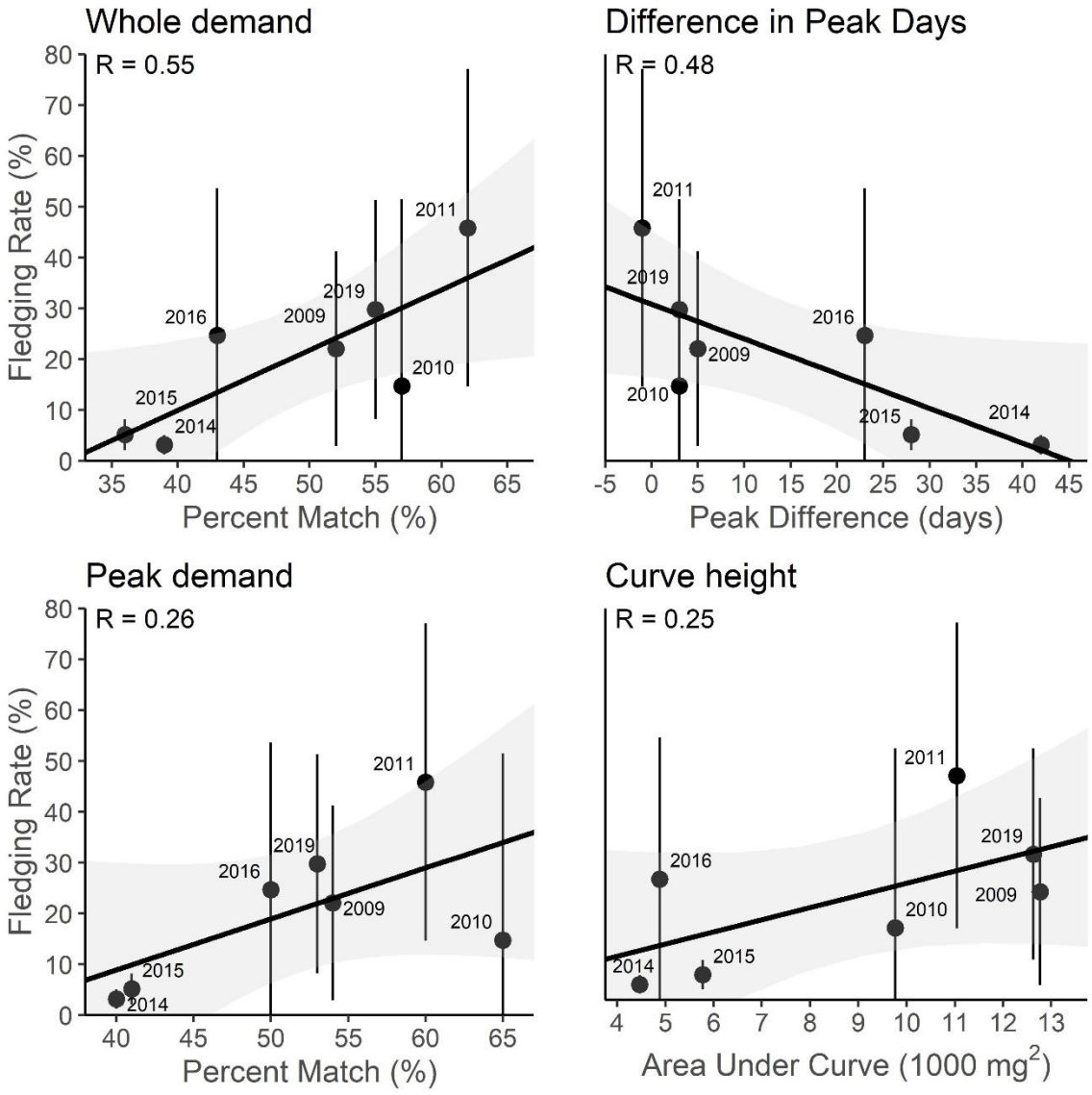

Figure 3.6. Correlation of annual Hudsonian godwit fledging rates with measures of whole demand overlap (upper left), difference in peak dates (upper right), peak demand overlap (lower left), and curve height (lower right). Annual fledging rates were extrapolated from daily survival rates with accompanying 95% credible intervals. Regression lines (black) with 95% confidence interval (grey) are shown. Correlation coefficient for univariate models is displayed for each model.

CHAPTER 4

CONCLUSION

Evidence of the variation in the effects ecological interactions across spatiotemporal contexts suggests that drawing broadly applicable conclusions requires a holistic assessment of the range of conditions in which they occur (Ferrari et al. 2019, Cassidy et al. 2020). Using Hudsonian godwit chicks as a case-study, I found that the relationships between godwit chicks and both their predators and prey change substantially throughout development. In my first chapter, I found that godwit chick survival was related to their con- and heterospecifics associations, but that the behavioral selection for group type in both space and time allowed godwit chicks to avoid the costs of higher predation risk. Then, in my second chapter, I showed the effects that resource availability has on individuals and populations depend on a given consumer's energetic needs at each timestep in the interaction. Taken together my research clarifies the influence that spatiotemporal context has on ecological interactions and underscores the necessity of observing behaviors across contexts before drawing conclusions about their effects (Chamberlain et al. 2014). Furthermore, the results I report here illustrate how studying intraindividual variation can deepen our understanding of the processes affecting animal behavior and population dynamics (Gårdmark and Huss 2020).

I found that the social associations godwits formed were more complex than previously thought, and, in fact, reflect a spatiotemporally variable landscape of risk.

Prey species adjust their habitat use according to perceived risk, thereby prioritizing the avoidance of some predators while tolerating others (Willems and Hill 2009, Królikowska et al. 2016, Palmer et al. 2017). Previous work in this system documented the differential effects of the godwit-gull association in the nesting and chick rearing phase (Swift et al. 2018). However, given the available data, it was assumed that gull avoidance was consistently optimal for young chicks. My results provide additional nuance to this view by documenting the role of conspecifics and age-dependent risks on the behaviors godwits employ and, especially, who they associate with. Following this work, we now know that godwits likely adjust their associations to avoid predator-related costs and that associating with conspecifics may facilitate this. Variable risk likely affects a species' optimal grouping behaviors and should be included when interpreting the costs and benefits of a given association (Mönkkönen et al. 2007, Morosinotto et al. 2012).

Importantly, information on how godwits contend with predators may become increasingly important as godwits both decline and experience alterations to the extant predators in their breeding habitats. The global population of godwits has declined by 3.4% annually since the 1970s (Rosenberg et al. 2019). In species that rely on conspecifics for habitat selection decisions, population declines can initiate Allee effects (i.e., negative density dependence; Stephens and Sutherland 1999, McLellan et al. 2010) to reinforce extinction processes (Gil et al. 2018). Meanwhile, the number and diversity of generalist predators that godwit chicks are exposed to is changing. For instance, coyotes (*Canus latrans*) expanded into the region surrounding Beluga as recently as the 1990s (Hody and Kays 2018). Coyotes now coexist and compete with the red foxes (*Vulpes vulpes*), common ravens (*Corvid corax*), great-horned owls (*Bubo virginianus*),

and sandhill cranes (*Grus canadensis*), all of whom prey upon godwits and other waterbirds (Schekkerman et al. 2009, Królikowska et al. 2016). An expanded community of generalist predators may affect the risk posed to godwits while avoiding the mew gulls, thus making conspecific associations even more valuable to godwit reproductive success (Chapman and Chapman 2000, Fletcher 2006). Through documenting the role of adaptive grouping behaviors in godwits' social behaviors, my work sheds early insights into the potential synergy between local- and larger-scale processes that require conservation attention.

In addition to establishing the link between population dynamics and the anti-predator behaviors godwits employ, my research also partly addresses the disconnect between the theoretical predictions and empirical results from tests of the match-mismatch hypothesis. In this system, godwit chicks were previously thought to be matched with resources (Senner et al. 2017); however, my work shows that age-dependent costs may hinder our ability to quantify the costs of mismatching from a single timepoint, such as when energetic demands are greatest. Growing energetic needs throughout development mean that older chicks face increasing costs of low-quality resources in addition to the constant costs of low-resource abundance. Furthermore, models that account for age-specific consumer demands improved our ability to explain interannual variation in godwit breeding success. Because all endotherms exhibit changing energetic needs as a function of time of year, environmental conditions, age, and reproductive status, accounting for this variation may be broadly important for predicting the consequences of mismatches on consumer populations (Ricklefs 2003, Tjørve et al. 2007).

Moreover, by viewing mismatching as a gradient, instead of as a categorical 'matched or mismatched' state, we stand to improve our ability to predict 'tipping points' in a species' response to mismatching. Consumer populations tolerate certain levels of mismatching, but can have thresholds past which the effects manifest (Simmonds et al. 2020, Samplonius et al. 2020). In godwits, our novel methods to identify apparent tipping points may be key to predicting their stability under future conditions. Here, I found that years with ~19% poorer overlap than the interannual mean can produce near complete reproductive failure in Beluga godwits. Given the godwit declines observed elsewhere in the Arctic (Senner et al. 2017), knowing the conditions under which populations fail to respond may be key to conservation planning.

Taken together, my research clarifies the possible synergy between top-down and bottom-up pressures driving animal behavior (Favreau et al. 2015, Bjornson and Anderson 2018). Times of poor resources can lead to higher predation risk as a result of prey or poorer condition (e.g., compensatory mortality; Vietrich et al. 2005, Mahoney et al. 2018). Given that as few as 13% of chicks in Beluga starve while the rest are depredated (Senner et al. 2017), the clear costs of low resource availability on body condition and survival I observed may indicate weakened chicks being more likely to be killed by predators. The resources and risks animals are exposed to likely interact to shape survival outcomes (Durant et al. 2007), suggesting that both need to be considered when drawing conclusions about the processes influencing individual- and population-level fitness.

Additionally, predators and resources may interact to affect optimal reproductive timing in godwits (Lima 2009). In general, animals time their reproductive events with

ephemeral resources and to avoid predation (Daugaard et al. 2019). Because predators living in community with their prey experience similar cues as well as take cues from their prey (Daugaard et al. 2019), predator synchrony may affect how species respond to environmental change (Latty and Dakos 2019). In the case of the godwits, both resources and predation risk appear to favor earlier reproduction, however that may not be true under all future scenarios. If, for example, the invertebrates of Beluga continue to become smaller or less abundant as they have in the past decade, the optimal timing of godwit hatch may cease to coincide with gulls, thereby negating the benefits godwits receive from their protective association with gulls. The decoupling of multiple trophic levels can disrupt species' ability to optimize their timing with respect to both resources and risk (Both et al. 2009). Given the fact that predation is the leading cause of reproductive failure in ground nesting birds (Forstmeier and Weiss 2004, Lima 2009), conflicting pressures may result in a catch-22 for godwits attempting to optimally time reproduction.

In general, my thesis suggests that viewing ecological interactions across contexts can provide insights into the variation in their effects. Exploring the processes responsible for inter- and intraindividual variation is key to learning how species' optimally respond to their environment (Cassidy et al. 2020). By updating our approach when asking ecological questions to prioritize observations of species' interactions across spatiotemporal contexts, we may be better suited for drawing broad conclusions about their effects on animal populations.

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APPENDIX A

SUPPLEMENTARY TABLES AND FIGURES TO "BEHAVIORAL ADJUSTMENTS IN THE ASSOCIATIONS OF A PRECOCIAL SHOREBIRD MEDIATE THE COSTS AND BENEFITS OF GROUPING DECISIONS"

Table A.1. Summary of Hudsonian godwit nest and chick sampling across study years in Beluga River, Alaska from early-May to mid-July each year.

Year	*Nests found*	*Nests hatched*	*No. chicks hatched*	*Radio tagged chicks*	*No. radio tagged chicks fledged*	*Resighting events ($\bar{x}$ (± SD))*	*Max days chick survived*
2009	24	19	65	18	5	4.0 (± 3)	11.0 (± 10)
2010	24	17	58	19	2	3.5 (± 3)	8.8 (± 8)
2011	28	21	72	23	11	4.4 (± 2)	12.3 (± 7)
2012*	32	20	-	-	-	-	-
2014	11	7	29	7	1	3.4 (± 2)	9.3 (± 5)
2015	18	13	45	18	2	3.6 (± 2)	10.4 (± 7)
2016	16	10	32	21	2	5.5 (± 2)	15 (± 7)
2019	16	15	48	22	8	5.4 (± 3)	13.9 (± 9)
All years	169	120	349	128	31	4.3 (± 3)	11.9 (± 8)

Table A.2. Summary data of covariates used in a mixed-effect cox proportional hazard model estimating the instantaneous risk of death of Hudsonian godwit chicks prior to fledge in Beluga River, Alaska.

Year	*Godwit hatch date ($\bar{x}$ (± SD))*	*Nearest neighbor distance (m)*	*Number of gull nests (<200m)*	*Distance to gull colony centroid (m)*	*Distance to forest edge (m)*
2009	4 Jun (± 2.9 d)	317 (± 186)	3.5 (± 3.1)	576 (± 2323)	520 (± 176)
2010	6 Jun (± 6.4 d)	472 (± 361)	4.5 (± 3.0)	622 (± 526)	478 (± 210)
2011	6 Jun (± 4.6 d)	292 (± 146)	3.0 (± 3.2)	706 (± 332)	484 (± 215)
2014	7 Jun (± 5.2 d)	553 (± 285)	4.6 (± 4.4)	541 (± 375)	438 (± 221)
2015	5 Jun (± 3.1 d)	320 (± 187)	4.7 (± 5.4)	539 (± 241)	402 (± 199)
2016	5 Jun (± 2.3 d)	204 (± 179.)	7.1 (± 5.6)	455 (± 179)	324 (± 198)
2019	5 Jun (± 4.5 d)	467 (± 417)	2.0 (± 3.0)	966 (± 571)	501 (± 258)
All years	5 Jun (± 4.3 d)	361 (± 298)	3.8 (± 4.2)	689 (±437)	458 (± 227)

Table A.3. Shapiro-Wilkes test of proportionality on the Schoenfeld residuals from a mixed-effect, time-to-event cox proportional hazards model performed on survival data from Hudsonian godwit chicks in Beluga River, Alaska from 2009 - 2019.

Predictor	X^2	*df*	*p-value*
Hatch date	2.64	5.00	0.75
Nearest neighbor distance	7.58	4.32	0.13
Brood density	0.05	4.02	1.00
Distance to gull colony centroid	0.23	4.3	0.96
Distance to forest edge	0.22	5.13	1.00
Number of nearby gull nests (<200m)	7.27	3.85	0.11
Global model	18.09	26.62	0.87

Table A.4. Spatial summary statistics and monitoring frequency of radio tagged Hudsonian godwit broods in the North plot near Beluga River, Alaska across sampling years. The single brood from 2014 was excluded due to low sample size.

					Early (<14 days)		*Late (≥14 days)*	
Year	*Number of broods*	*Locations per brood ($\bar{x}$ ± SD)*	*Days between successive locations*	*Distance travelled between successive locations (m)*	*KUD² area (km²) ($\bar{x}$ ± SE)*	*Number of broods*	*KUD area*	*Number of broods*
2009	7	6 (± 0.93)	1.75 (± 1.03)	391 (± 306)	1.43 (± 0.50)	4	2.64 (± 1.52)	2
2010	4	7 (± 0.84)	2.29 (± 1.22)	326 (± 262)	1.90 (± 0.74)	2	0.60 (± 0.21)	2
2011	12	7 (± 0.83)	1.15 (± 0.55)	324 (± 269)	1.74 (± 0.42)	12	0.66 (± 0.29)	4
2014	1	4	0.55 (± 0.32)	225 (± 127)	-	-	-	-
2015	12	11 (± 0.69)	0.87 (± 0.52)	371 (± 284)	1.65 (± 0.33)	9	1.07 (± 0.25)	3
2016	4	21 (± 0.46)	0.88 (± 0.26)	443 (± 423)	2.30 (± 0.95)	4	2.52 (± 1.39)	3
2019	9	16 (± 0.57)	1.16 (± 0.27)	382 (± 423)	2.29 (± 0.81)	9	3.22 (± 1.55)	4
All Years	49	11 (± 8.89)	1.07 (± 0.49)	373 (± 344)	1.87 (± 0.23)	44	1.82 (± 0.47)	18

Table A.5. Model selection table from a mixed-effect cox proportional hazards model to estimate the instantaneous risk of death of Hudsonian godwit chicks prior to fledge during 2009 – 2019 monitoring near Beluga River, Alaska. Model selection was done within the package 'MuMIn' on all combinations of standardized predictor variables. Model's with $\Delta_{AICc} < 4$ and the intercept only model are reported, organized by descending Δ_{AIC} value. Plus signs (+) indicate the inclusion within the model.

Model no.	*Nearest neighbor distance*	*Nest hatch date*	*Dist. to gull colony centroid*	*No. nearby gull nests*	*Brood density*	*Dist. to forest edge*	*df*	*AICc*	Δ_{AICc}	*Model weight*
30	+	+	+	+			4	627.9	0	0.381
32	+	+	+	+	+		5	629.4	1.46	0.184
62	+	+	+	+		+	5	629.4	1.52	0.178
64	+	+	+	+	+	+	6	630.5	2.64	0.102
22	+	+	+				3	630.6	2.72	0.098
24	+	+	+		+		4	631.7	3.79	0.057
1							14	679.5	51.55	0.000

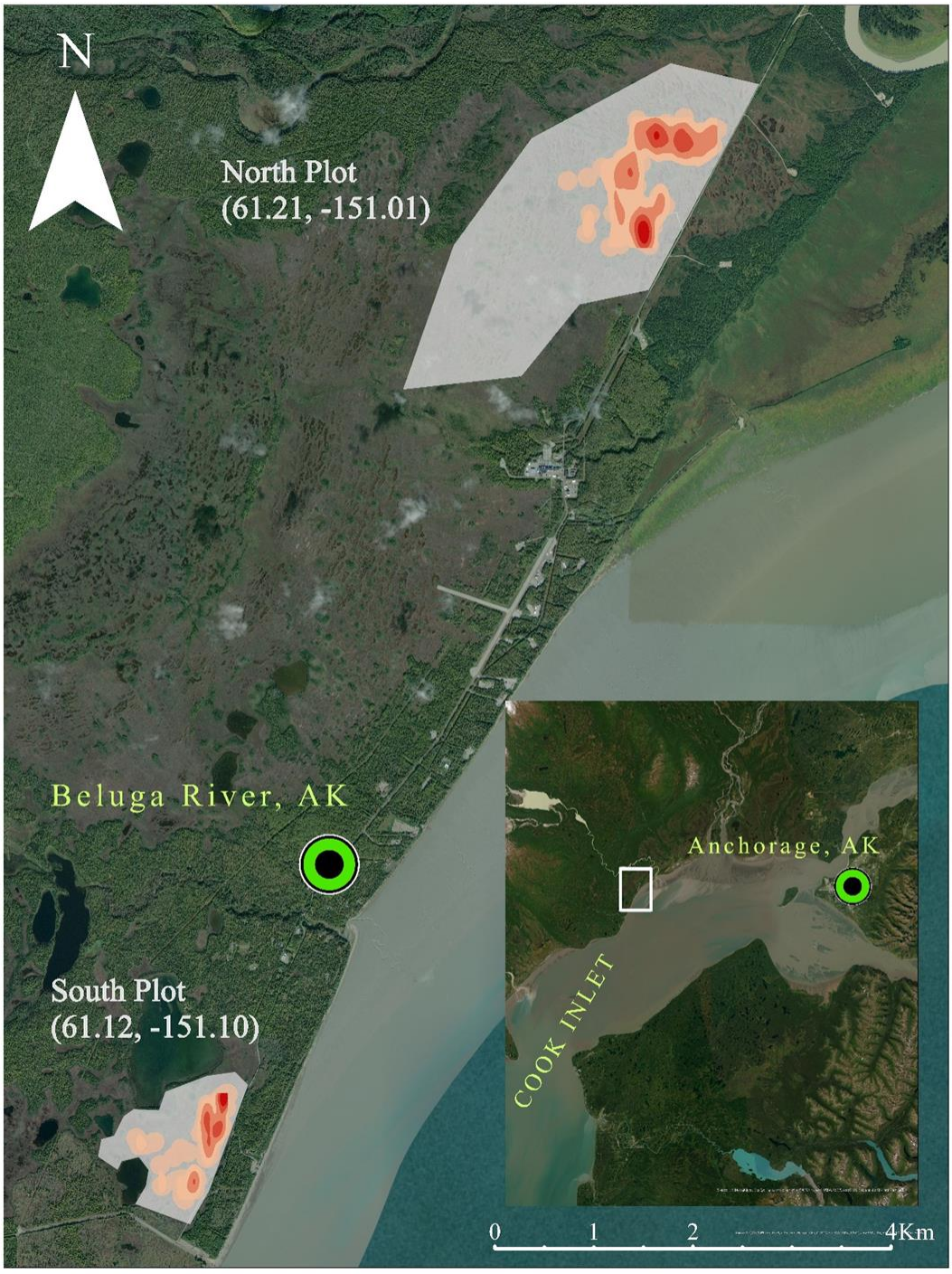
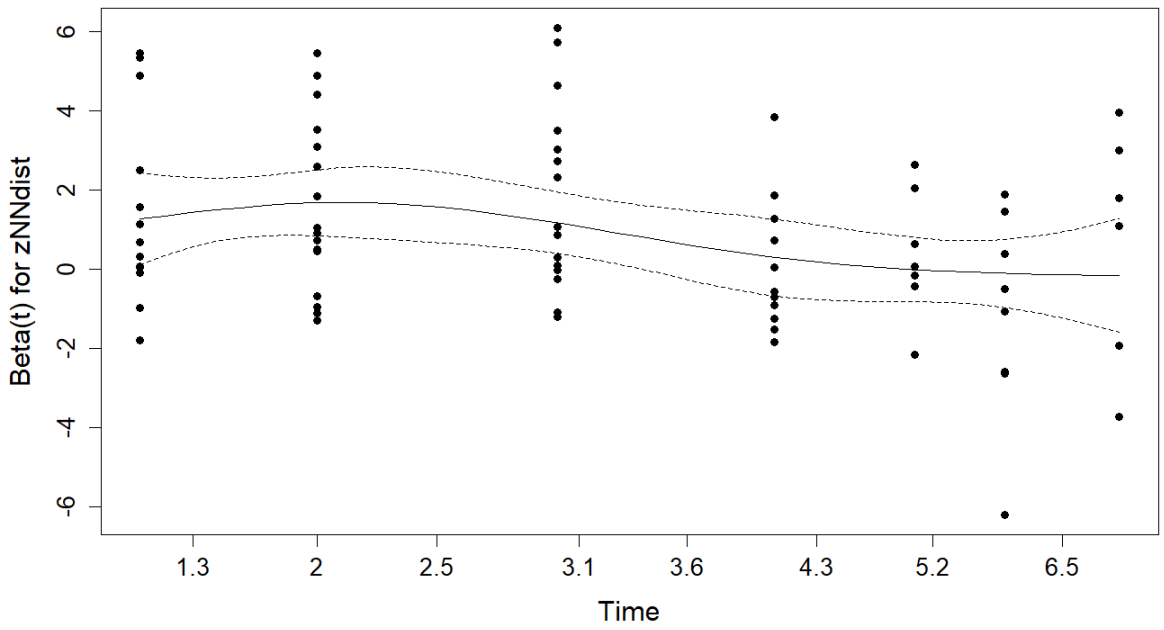


Figure A.1. Location of North and South mew gull colonies (red) are shown as kernel density contours (dark red is high use, light red is low use) within the North and South study plots (grey polygons) near the township of Beluga River, Alaska (green circle). Darker red represents higher density values. Plots are 5.5 and 1.2 km^2 respectively and

are separated by ~7 km of unmonitored bog and boreal forest. (Inset) Location of study region (white square) in relation to the Cook Inlet and the city of Anchorage, AK (green circle).


Beta(t) for zNNdist
6
4
2
0
-2
-4
-6
1.3
2
2.5
3.1
3.6
4.3
5.2
6.5
Time

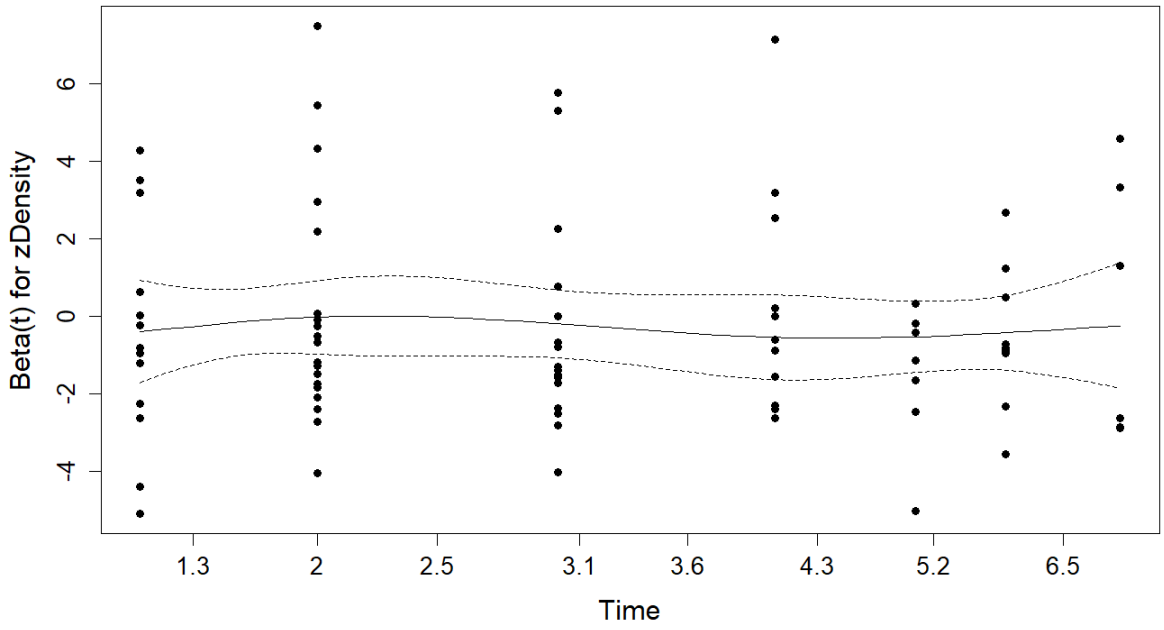
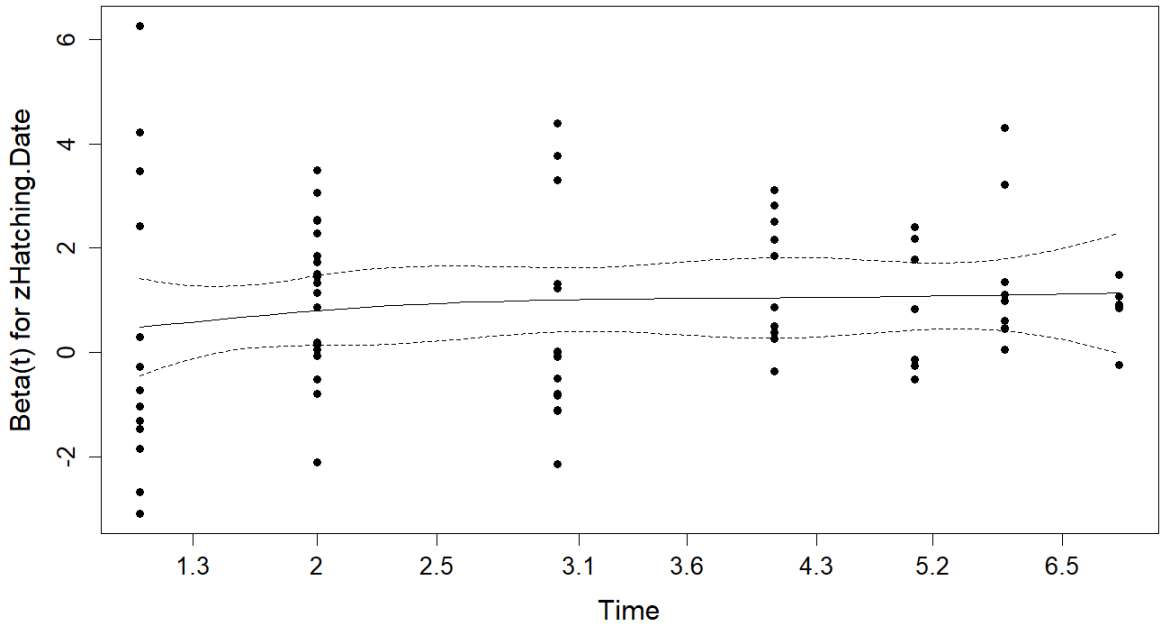

Beta(t) for zDensity
6
4
2
0
-2
-4
1.3
2
2.5
3.1
3.6
4.3
5.2
6.5
Time

Figure A.2



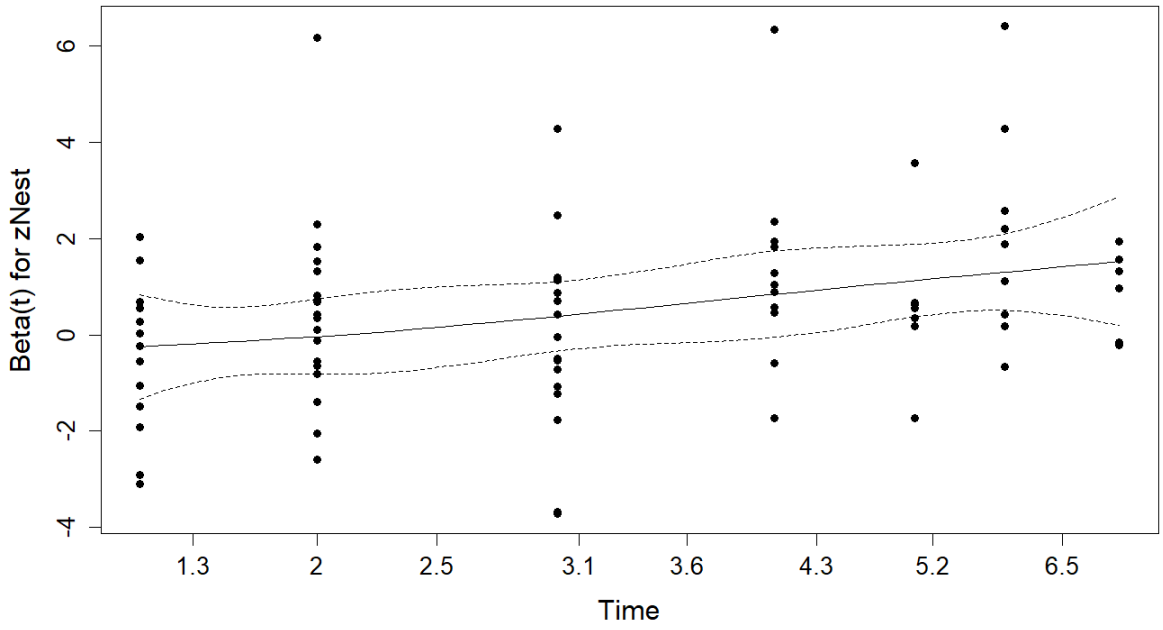


Figure A.2 (cont.)

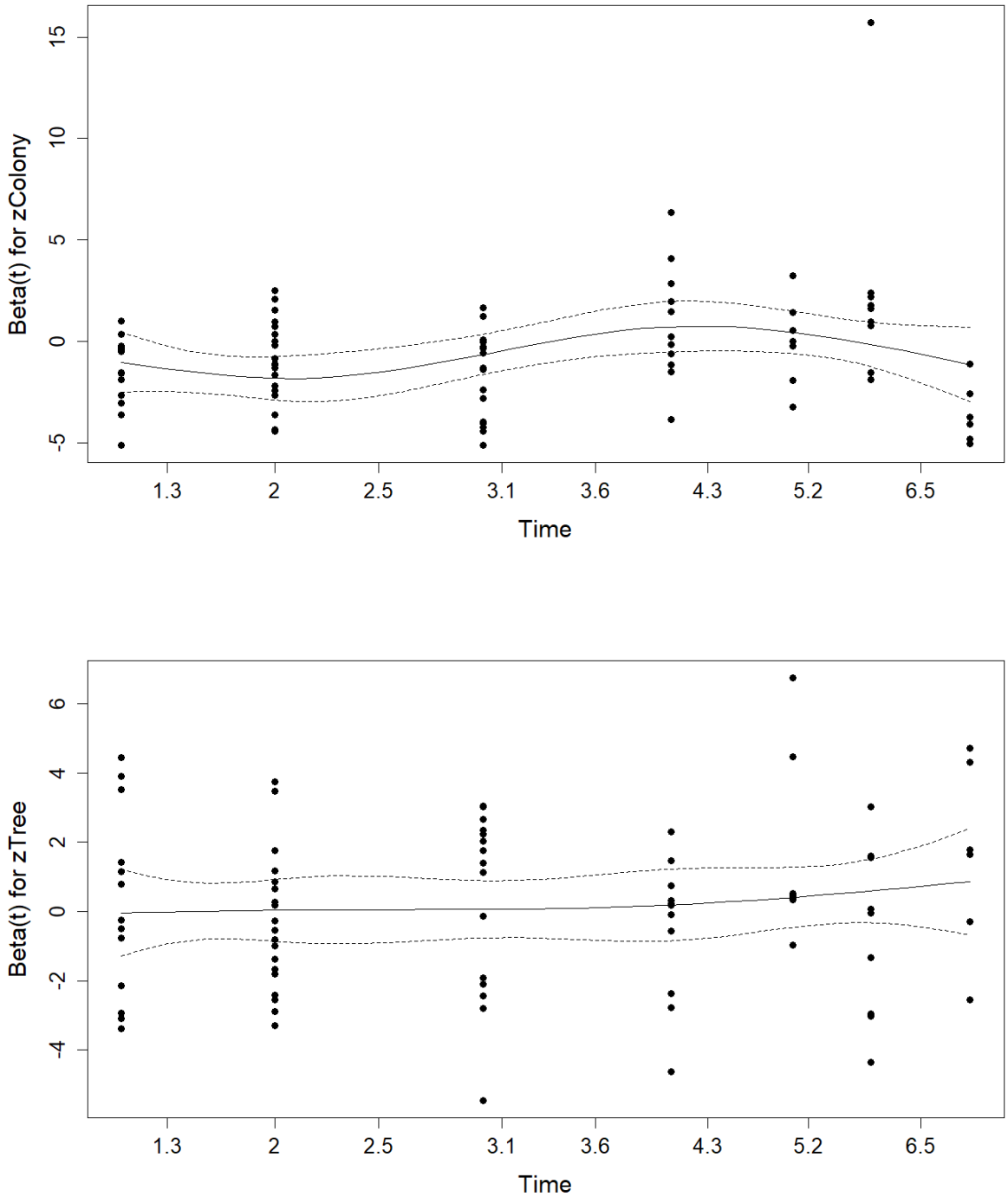


Figure A.2. The Schoenfeld residuals of each predictor – (in order, top to bottom) [1] nearest neighbor distance between tagged chicks, [2] daily brood density, [3] nest hatch date, [4] Euclidian distance to gull colony centroid, [5] number of gull nests within 200 m, and [6] distance to forest edge – across time intervals in the mixed-effect Cox proportional hazards model performed with survival data from Hudsonian godwit chicks

in Beluga River, Alaska. Lack of a trend is evidence for proportionality (i.e., constant predictor effects) in the model covariates. Covariates were rescaled to z values by dividing by 2 standard deviations.

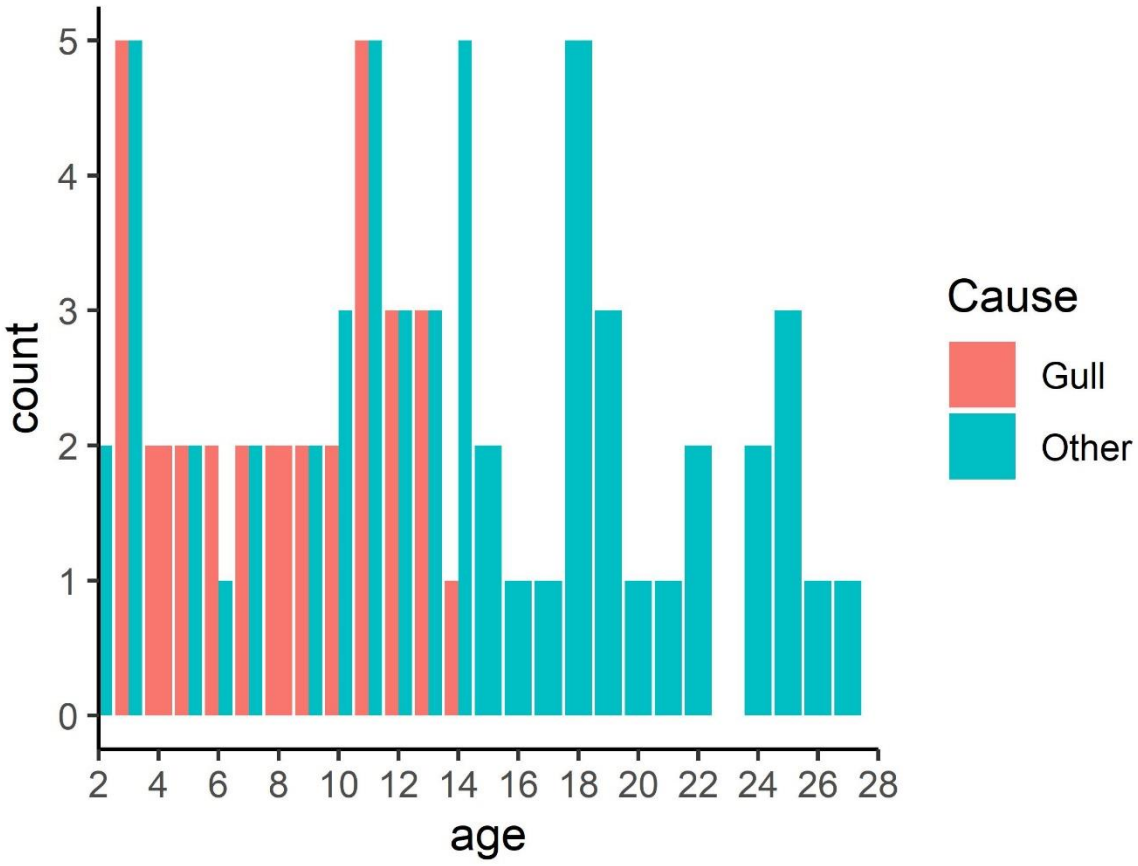


Figure A.3. Number of predator related Hudsonian godwit chick mortalities directly attributable to gulls (red; i.e., on or within 25 m of a mew gull nest) and attributed to other predators (blue) in Beluga River, Alaska by age.

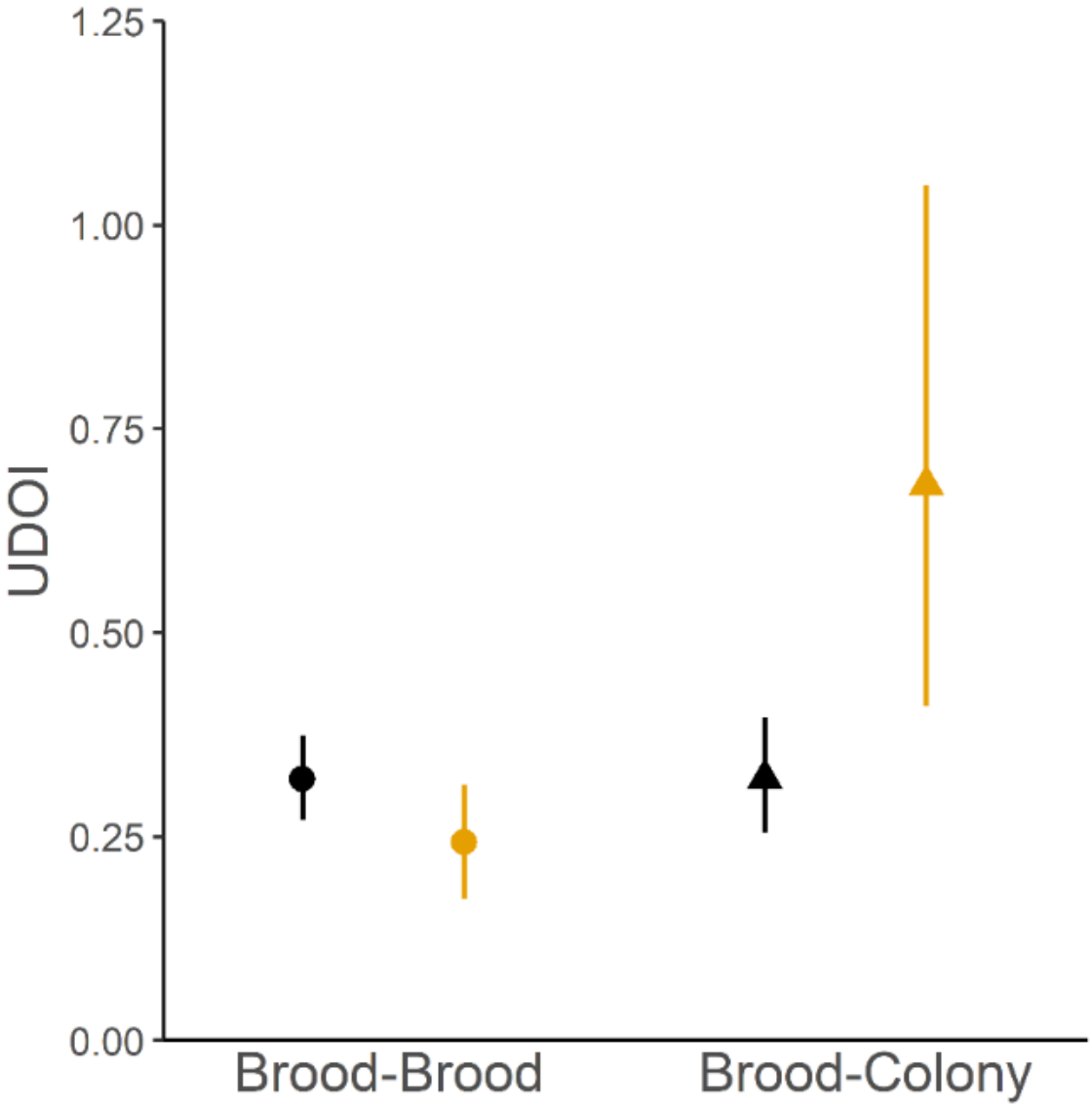


Figure A.4. Space use sharing between Hudsonian godwit broods (circles; n = 342) and with the gull colony (triangles; n = 116) in Beluga River, Alaska. Higher utilization distribution overlap index (UDOI) values (y–axis) indicate a higher degree of overlap, and UDOI > 1 indicate complete space use sharing. Brood–Brood: UDOI between broods during the first 14–days of the pre–fledge period (early, black circle; $n_{B–B}$ = 302) and last 14–days (late, yellow circle; $n_{B–B}$ = 40). Brood–Colony: UDOI of broods with the year–specific gull colony during the early (black triangle; $n_{B–C}$ = 80) and late period (yellow triangle; $n_{B–C}$ = 36). Mean estimates of pairwise UDOI are shown with bootstrapped 95% confidence intervals (n = 100).

APPENDIX B

SUPPLEMENTARY TABLES AND FIGURES TO "THE ANATOMY OF A PHENOLOGICAL MISMATCH: INTERACTING CONSUMER DEMAND AND RESOURCE CHARACTERISTICS DETERMINE THE CONSEQUENCES OF MISMATCHING

Table B.1. Estimates of Pearson's correlation coefficient (r) among pairs of fixed effect covariates in a generalized additive mixed model predicting godwit chick body condition index estimates collected in Beluga River, Alaska from 2009–2019.

Variable 1	*Variable 2*	*r*	*lower*	*upper*
Size	Insect	0.22	0.01	0.41
Size	Hatch	0.27	0.07	0.46
Insect	Hatch	0.04	-0.17	0.24

Table B.2. Estimates of Pearson's correlation coefficient (r) among pairs of fixed effect covariates in a Bayesian hierarchical model on the survival of Hudsonian godwit chicks living near Beluga River, Alaska (2009–2019). Coefficients were measured to check collinearity between predictors in a global model prior to model selection procedures.

Variable 1	*Variable 2*	*r*	*lower*	*upper*
Size	Chick age	-0.006	-0.04	0.03
Size	Insect	0.32	0.78	0.36
Size	Chick hatch date	-0.05	-0.09	-0.01
Insect	Chick age	-0.03	-0.08	0.02
Insect	Chick hatch date	0.07	0.02	0.11
Chick hatch date	Chick age	-0.04	-0.06	-0.01

Table B.3. Summary of season lengths and the observed Hudsonian godwit hatching dates and model predicted invertebrate resource peak from 2009 – 2019 near Beluga River, Alaska. The resource peak was calculated as the day with the smallest first derivative along the day + day^2 curve. Neither godwits or invertebrates were monitored for the full 2012 or 2017 season.

Year	*No. chicks hatched*	*Dates of study*	*Mean hatch date (± SD)*	*Predicted resource peak*
2009	69	3 May – 10 Jul	5 Jun (± 5.5 d)	5 Jun
2010	60	3 May – 10 Jul	11 Jun (± 9.4 d)	8 Jun
2011	87	3 May – 10 Jul	7 Jun (± 5.0 d)	14 Jun
2012	32	8 May – 5 Jun	9 Jun (± 5.0 d)	-
2014	31	9 May – 13 Jul	9 Jun (± 5.6 d)	10 May
2015	62	3 May – 10 Jul	6 Jun (± 3.2 d)	31 May
2016	38	1 May – 10 Jul	5 Jun (± 4.0 d)	20 May
2017	-	11 May – 19 May	-	-
2019	56	6 May – 26 Jul	7 Jun (± 5.3 d)	11 Jun

Table B.4. Model selection table of logistic models predicting godwit chick mass from weekly captures (n = 103) of godwit chicks near Beluga River, Alaska from 2009−2019. Following Senner et al. (2017) asymptotic mass was set to the adult average (~249 g). Initial values were set prior to modeling: inflection point T_i=10.7, logistic coefficient K=0.12. Chick identity (ID) was included as a random intercept for variables (✓), and all models had at least one random intercept term. Parameter estimates were averaged from 100 iterations. AIC_c = Akaike's Information Criterion corrected for small sample sizes.

Model no.	*Var.*	*Value*	*Chick ID random intercept*	*ΔAIC_c*	*log-likelihood*	*Model weight*	*No. parameters*
2	T_i	~1	✓	0.0	-528.0	0.98	6
	K	~1	✓				
4	T_i	~year	✓	6.9	-528.5	0.02	9
	K	~1					
10	T_i	~year	✓	11.7	-525.9	>0.01	14
	K	~year					
1	T_i	~1	✓	17.5	-538.3	>0.01	4
	K	~1					
8	T_i	~1	✓	21.2	-535.6	>0.01	9
	K	~year					
5	T_i	~year		35.5	-542.8	>0.01	9
	K	~1	✓				
11	T_i	~year		40.0	-540.1	>0.01	14
	K	~year	✓				
7	T_i	~1		78.8	-564.5	>0.01	9
	K	~year	✓				
3	T_i	~1		80.7	-570.4	>0.01	4
	K	~1	✓				
9	T_i	~1	✓	136.4	-593.1	>0.01	9
	K	~year	✓				
12	T_i	~year	✓	183.5	-602.4	>0.01	14
	K	~year	✓				
6	T_i	~year	✓	188.4	-605.2	>0.01	9
	K	~1	✓				

Table B.5. Model selection table of random intercept terms (top) and the timescale of continuous covariate (bottom) in our global generalized additive mixed model to predict body condition index of godwit chicks near Beluga River, Alaska from 2009 − 2019. Timescale is the period over which the continuous fixed effect variables – daily invertebrate biomass and daily median invertebrate body size – in the global model were averaged for model smoothing. AIC_c = Akaike's Information Criterion corrected for small sample sizes.

Random intercepts				
	ΔAIC_c	*Deviance*	*Model weight (w_i)*	*No. parameters*
~ 1	0	11.6	0.42	4
~ 1|chick	4.2	14.5	0.22	59
~ 1|brood + 1|chick	5.0	16.1	0.17	51
~ 1|year	5.2	17.5	0.10	9
~ 1|year + 1|brood	7.8	19.0	0.04	52
~ 1|brood	8.1	19.3	0.03	47
~ 1|year + 1|chick/brood	11.9	23.5	>.01	64

Timescale				
	ΔAIC_c	*Deviance*	*Model weight (w_i)*	*log-Likelihood*
7-day avg.	0	12.7	0.69	-39.6
3-day avg.	2.3	13.0	0.22	-40.8
day of	4.7	134	0.06	-42.0
1-day avg.	6.4	13.6	0.03	-42.8

Table B.6. Comparison by AIC_c value among candidate models with predictor variables of Hudsonian godwit chick growth (n = 89) from 2009–2019, excluding chicks from 2014 (which lacked recaptures). Growth was estimated from body condition index (BCI) scores obtained from weekly captures. Continuous predictors were averaged over a 7-day period prior to BCI estimation. Inclusion in a model is indicated by a beta coefficient for predictors and plus signs (+) for chick age smoothing term. AIC_c = Akaike's Information Criterion corrected for small sample sizes.

Intercept	*Invertebrate biomass*	*Invertebrate body size*	*Chick hatch date*	*s(Chick age)*	*df*	*log-likelihood*	*AIC_c*	*ΔAIC_c*	*Model weight*
0.445	0.006		-0.254	+	10	-22.915	70.651	0	0.75
0.396	0.006	0.019	-0.264	+	12	-22.506	73.095	2.444	0.22
0.498	0.006			+	8	-30.107	79.422	8.771	0.01
0.507	0.006		-0.22		3	-35.684	79.838	9.188	0.01
0.578	0.006	-0.034		+	9	-29.768	81.256	10.605	0.004
0.428	0.005	0.032	-0.233		5	-35.494	81.701	11.051	0.003
0.517	0.005				3	-39.643	85.564	14.914	0
0.541	0.005	-0.01			4	-39.626	87.722	17.071	0
0.929			-0.198	+	7	-38.597	94.041	23.39	0
0.714		0.075	-0.237	+	8	-37.562	94.675	24.025	0
0.929				+	6	-41.381	97.02	26.369	0
0.929			-0.206		3	-45.415	97.109	26.458	0
0.696		0.082	-0.241		3	-44.356	97.183	26.533	0
0.854		0.027		+	7	-41.299	99.125	28.474	0
0.929					2	-48.25	100.639	29.988	0
0.817		0.039			2	-48.003	102.284	31.633	0

Table B.7. Group levels (i.e., random effects) from a Bayesian hierarchical model predicting the daily survival rate of Hudsonian godwit chicks from 2009–2019 near Beluga River, Alaska. $\hat{R}$ is the Gelman-Rubin statistic where $\hat{R}<1.1$ is evidence of convergence. Individual histories were grouped by study year, brood, and plot.

Group level	*Posterior mean (SD)*	*95% Credible Interval*	*Effective sample size*	$\hat{R}$
2009	0.05 (13.64)	-28.12, 30.87	14279	1.0
2010	0.01 (13.67)	-28.99, 29.99	15274	1.0
2011	0.1 (13.49)	-30.53, 27.12	15000	1.0
2014	-0.15 (13.37)	-28.87, 27.64	15000	1.0
2015	0.05 (13.6)	-28.91, 28.86	15167	1.0
2016	0.08 (7.13)	-23.6, 2.56	14041	1.1
2019	0.11 (6.1)	-12.08, 11.35	14901	1.2
2009GN001	0.14 (8.86)	-17.3, 18.24	15000	1.0
2009GN002	0.06 (8.76)	-17.72, 17.84	16088	1.0
2009GN003	-0.08 (8.67)	-17.92, 16.96	14798	1.0
2009GN007	0.11 (8.69)	-17.57, 17.56	16964	1.0
2009GN010	-0.02 (8.73)	-17.27, 17.91	15639	1.0
2009GN012	0.11 (8.56)	-16.36, 18.09	14182	1.0
2009GN014	0.02 (8.76)	-18.02, 17.25	14961	1.0
2009GN018.2	0 (8.73)	-17.93, 17	14634	1.0
2009GN022	-0.01 (8.65)	-18.94, 16.39	15000	1.0
2009GN027	-0.01 (8.67)	-17.87, 16.76	14758	1.0
2009GN0282	0.08 (8.63)	-17.23, 17.5	15000	1.0
2009GN044	-0.1 (8.71)	-17.64, 17.27	14861	1.0
2009GN045	-0.1 (8.78)	-18.39, 16.86	16001	1.0
2009GN046	-0.2 (8.7)	-18.62, 16.41	14546	1.0
2009GN047	0 (8.59)	-16.63, 17.95	15000	1.0
2009GN049	0.03 (8.62)	-17.17, 17.34	15000	1.0
2010GN11	-0.02 (8.7)	-17.03, 17.74	14803	1.0
2010GN47	0.02 (8.81)	-18.13, 17.77	14507	1.0
2010GN58	-0.06 (8.77)	-18.62, 17.25	14934	1.0
2010GN61	-0.04 (8.75)	-18.04, 17.51	14517	1.0
2010GN62	0.02 (8.7)	-17.51, 17.35	14532	1.0
2010GN63	-0.06 (8.7)	-17.69, 17.42	15466	1.0
2010GNGPM	-0.1 (8.59)	-18.01, 16.85	15080	1.0
2010GNHUYU	-0.01 (8.67)	-18.03, 17.33	15000	1.0
2010GNPE	-0.01 (8.74)	-17.29, 18.19	14097	1.0
2010GNUL	0.01 (8.78)	-18.5, 16.97	15142	1.0
2010GNXEXY	0.1 (8.63)	-16.61, 17.69	15418	1.0
2010GNYN2	0.07 (8.64)	-17.32, 17.49	16213	1.0
2010GNYTXL	-0.01 (8.51)	-18.03, 16.35	14345	1.0
2011GN13	-0.01 (8.67)	-17.26, 17.53	15000	1.0
2011GNAPAU	-0.07 (8.74)	-18.48, 16.33	15215	1.0
2011GNC4T6	-0.09 (8.7)	-17.62, 17.25	15352	1.0
2011GNC8J2	0 (8.71)	-17.68, 17.39	15627	1.0
2011GNCT	-0.03 (8.65)	-17.23, 17.63	14886	1.0
2011GNE5E9	-0.01 (8.66)	-18.19, 16.62	16547	1.0

2011GNEAE7	0.02 (8.71)	-17.49, 17.98	15237	1.0
2011GNEE	-0.1 (8.68)	-17.61, 17.29	15149	1.0
2011GNH7T2	-0.02 (8.79)	-18.41, 17.55	15870	1.0
2011GNH8LO	-0.02 (8.69)	-17.94, 17.17	15000	1.0
2011GNJ5K7	-0.06 (8.63)	-17.96, 16.89	15812	1.0
2011GNJ6J0	-0.01 (8.76)	-17.6, 17.41	15054	1.0
2011GNJTMU	-0.15 (8.72)	-17.57, 17.3	14835	1.0
2011GNK0PM	-0.02 (8.69)	-18.08, 16.74	15140	1.0
2011GNK4T7	0.04 (8.68)	-17.54, 17.8	14034	1.0
2011GNM2P2	0.06 (8.59)	-17.17, 17.36	15133	1.0
2011GNM3U0	-0.05 (8.56)	-17.72, 16.9	14778	1.0
2011GNN8X3	0.05 (8.85)	-17.29, 18.38	14942	1.0
2011GNTANA	-0.1 (8.67)	-17.42, 17.53	15048	1.0
2011GNV9C0	0.1 (8.66)	-17.55, 17.17	15378	1.0
2011GNX50H	-0.04 (8.69)	-17.13, 17.56	17680	1.0
2011GNX6H3	0 (8.75)	-17.21, 18.3	15552	1.0
2011GNY9L6	0.05 (8.69)	-17.11, 17.55	14683	1.0
2014BHD17	-0.09 (8.65)	-16.81, 18.31	15443	1.0
2014BHD19	0.06 (8.56)	-17.82, 16.69	15000	1.0
2014BJL17	0.03 (8.74)	-17.33, 17.81	14793	1.0
2014BJL18	0.08 (8.62)	-16.91, 17.5	15561	1.0
2014BJL19	0.01 (8.74)	-16.72, 18.86	14404	1.0
2014BJL25	0.12 (8.63)	-18.14, 16.59	15273	1.0
2014GJM06	-0.11 (8.65)	-16.67, 18.44	15000	1.0
2015GJM05	0.08 (8.6)	-16.51, 18.2	15402	1.0
2015GJM18	-0.03 (8.65)	-17.03, 18.23	15705	1.0
2015GJM35	0.09 (8.66)	-17.71, 17.12	15000	1.0
2015GJM36	-0.02 (8.59)	-17.06, 17.39	14401	1.011
2015JAK05	0.04 (8.66)	-17.56, 17.46	14887	1.0
2015JAK21	0.01 (8.71)	-16.73, 18.05	16195	1.0
2015JMH10	0.01 (8.76)	-18.48, 16.96	15801	1.0
2015JMH20	0.1 (8.82)	-17.38, 18.13	15056	1.0
2015JMH28	0.01 (8.81)	-18.11, 17.84	16209	1.0
2015KJP18	-0.01 (8.68)	-18.69, 16.75	14590	1.0
2015KJP44	0.08 (8.63)	-16.9, 17.92	15242	1.0
2015RJS05	-0.03 (8.57)	-18.11, 16.63	14870	1.0
2015RJS05	0.01 (8.62)	-16.81, 17.7	15000	1.0
2015U1MUV	-0.08 (8.74)	-18.08, 17.02	15000	1.0
2016KRS48	-9.52 (7.63)	-23.78, 7.31	12247	1.02
2016LKF04	0.56 (8.09)	-15.47, 16.61	13272	1.0
2016LKF22	0.01 (7.83)	-14.38, 15.86	15014	1.01
2016MLS14	0.93 (7.97)	-15.23, 16.6	13951	1.0
2016MLS37	1.58 (6.71)	-11.8, 15.43	12726	1.01
2016RIG15	-0.33 (6.32)	-12.24, 13.79	12952	1.01
2016RJS04	0.4 (7.66)	-13.98, 16	12602	1.0
2016RJS07	0.16 (7.88)	-14.45, 16.73	12428	1.01
2016RJS10	-3.46 (5.03)	-14.37, 6.13	12259	1.08
2016RJS16	3 (7.09)	-11.12, 17.81	12935	1.02
2019GB01	-7.09 (3.08)	-13.5, -1.65	14744	1.01

2019GB02	-2.31 (4.56)	-11.09, 7.26	14948	1.05
2019GB03	-7.96 (4.41)	-15.49, 1.97	13044	1.07
2019GN01	1.6 (4.38)	-6.11, 11.44	15159	1.08
2019GN02	10.11 (5.97)	-0.66, 22.54	15057	1.02
2019GN03	-8.88 (4.4)	-16.79, 0.63	13173	1.07
2019GN05	2.89 (6.6)	-7.96, 16.62	14273	1.04
2019GN06	8.15 (5.67)	-2.12, 19.74	14424	1.01
2019GN08	0.65 (2.99)	-5.79, 5.92	13055	1.01
2019GN09	6.69 (6.41)	-6.64, 19.79	12900	1.01
2019GN10	-3.69 (6.79)	-15.05, 11.02	12128	1.01
2019GN11	-5.76 (3.11)	-12.24, 0.12	13962	1.02
2019GN12	8.23 (5.62)	-1.68, 19.93	14157	1.01
South Plot	0.26 (4.43)	-8.25, 9.21	14071	1.16
North Plot	3.28 (4.78)	-3.97, 14.22	12493	1.02

Table B.8. Annual daily survival rates (DSR) of Hudsonian godwit chicks (*n*=122) in Beluga River, Alaska among study years. DSR estimates from a Bayesian hierarchical model were extrapolated to 28 days as an estimate of percent fledged, and associated delta error is reported.

Year	*No. godwit chicks*	*DSR (mean)*	*SD*	*95% credible interval*	*% chicks fledged (± Delta error)*
2009	16	0.931	0.088	0.871, 0.964	22.11 (±19.13)
2010	16	0.913	0.178	0.810, 0.963	14.75 (±36.69)
2011	24	0.964	0.072	0.929, 0.982	45.84 (±21.22)
2014	07	0.849	0.174	0.672, 0.939	3.18 (±1.88)
2015	17	0.868	0.139	0.781, 0.924	5.16 (±3.00)
2016	20	0.936	0.097	0.890, 0.963	24.71 (±28.95)
2019	22	0.944	0.070	0.906, 0.967	29.79 (±21.54)

Table B.9. Model selection table comparing univariate linear models of population mismatch models predicting annual fledging rates in a population of Hudsonian godwits near Beluga River, Alaska from 2009–2019. AIC_c = Akaike's Information Criterion corrected for small sample sizes.

Model	*log-likelihood*	*AIC_c*	*ΔAIC_c*	*Model weight*	*R^2*
Whole Demand	-25.14	64.27	0	0.43	0.55
Difference in peak dates	-25.31	64.63	0.35	0.36	0.48
Peak Demand	-28.54	67.08	2.81	0.11	0.26
Curve height	-26.62	67.23	2.96	0.10	0.25

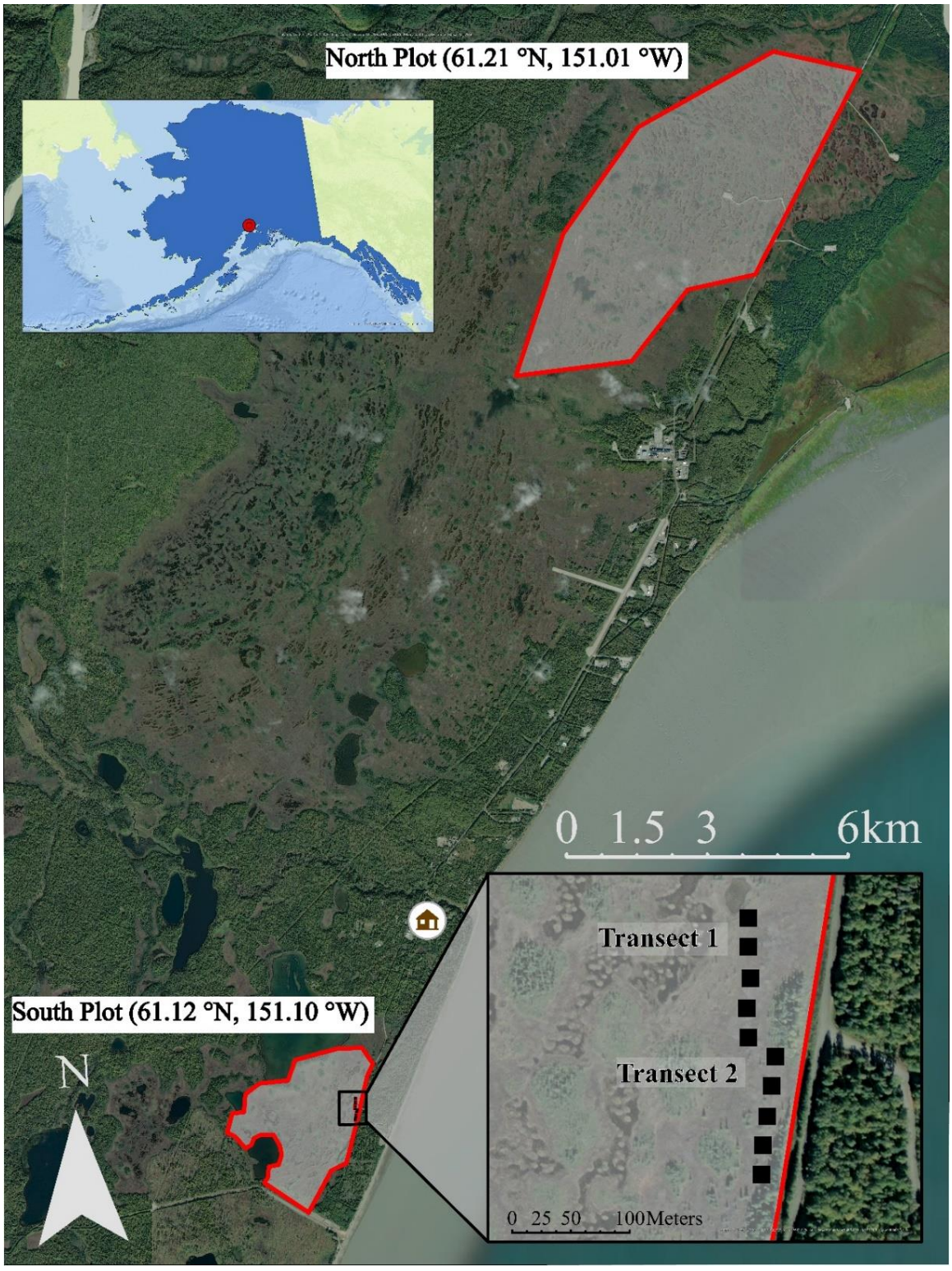


Figure B.1. Map of North and South plots (red polygons) near the township of Beluga River, Alaska (house icon). (Inset top left) The study areas (red point) is located in southcentral Alaska on the west coast of the upper Cook Inlet. (Inset bottom right) The

two, 100-m transects for daily invertebrate capture using pitfall traps (2009−2011) or modified malaise traps (2014−2016, 2019). Transects were placed according to Arctic Shorebird Demographic Network protocols (Brown et al. 2014). Basemap images are the intellectual property of Esri and are used herein under license. Copyright © 2014 Esri and its Licensors. All rights reserved. Additional data sources: U.S. Census Bureau 2018.

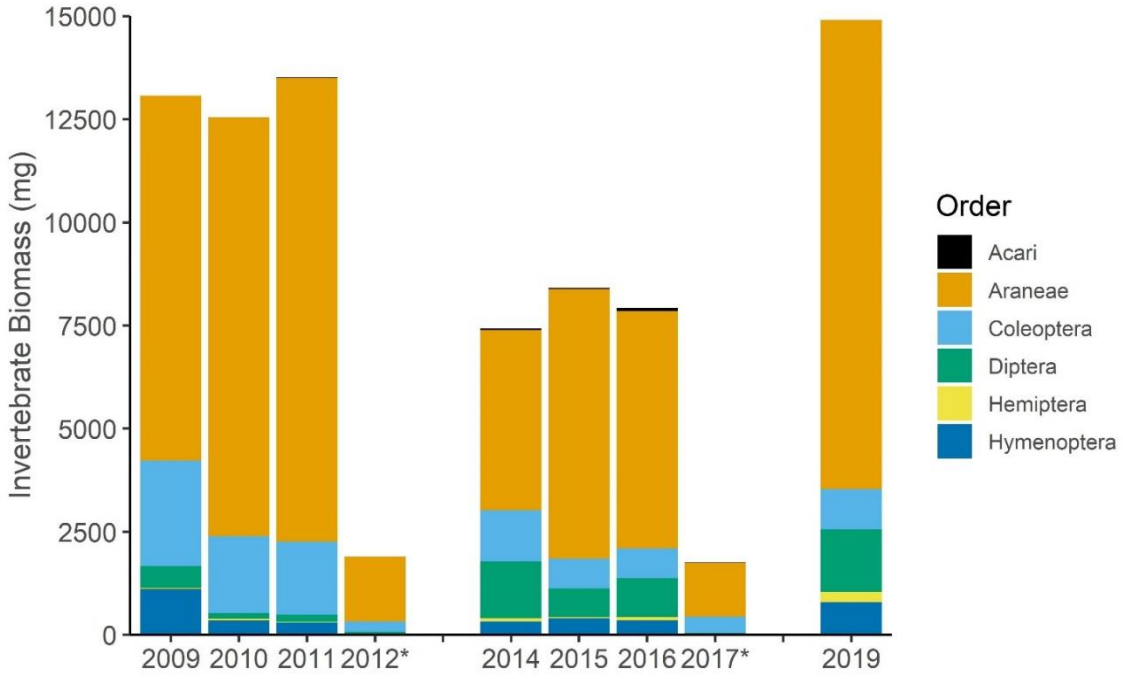


Figure B.2. Interannual comparison of the available biomass and composition by each of the six major Orders available near Beluga River, Alaska. Invertebrates were monitored daily from 2009−2019. Biomass was estimated using published, taxon-specific length-weight relationships. The 2012 and 2017 seasons (*) were short seasons and do not represent the extent of the available invertebrate community. No monitoring occurred in 2013 and 2018.

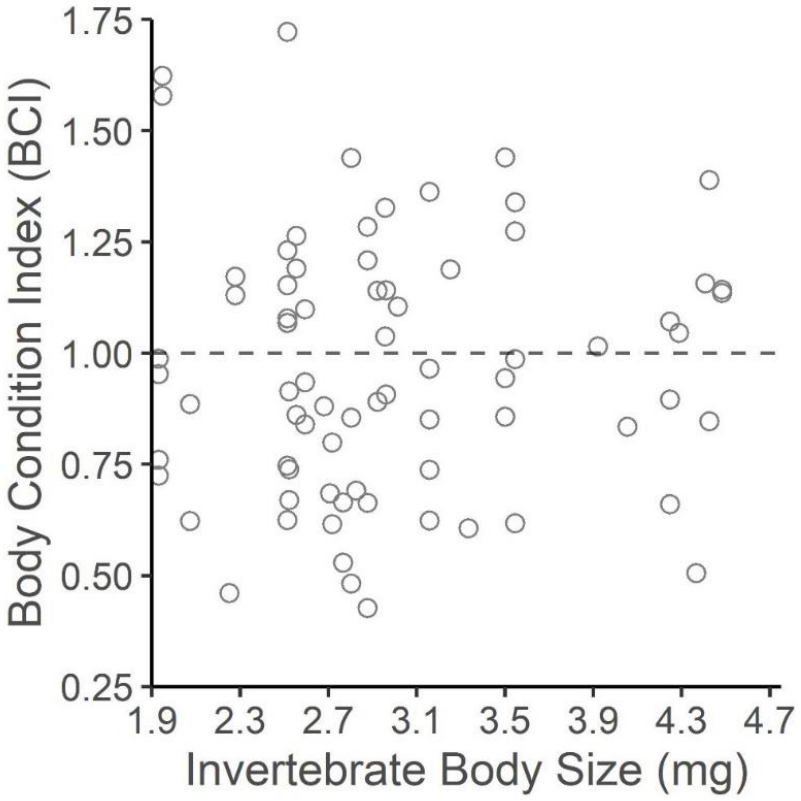


Figure B.3. Effect of median invertebrate body size (mg) on the body condition index (BCI) of Hudsonian godwit chicks monitored near Beluga River, Alaska from 2009 - 2019. BCI is the ratio of observed to expected weight gain. BCI=1 (dashed line) means individuals grew as expected, while BCI>1 and BCI<1 indicate better or worse than predicted, respectively.

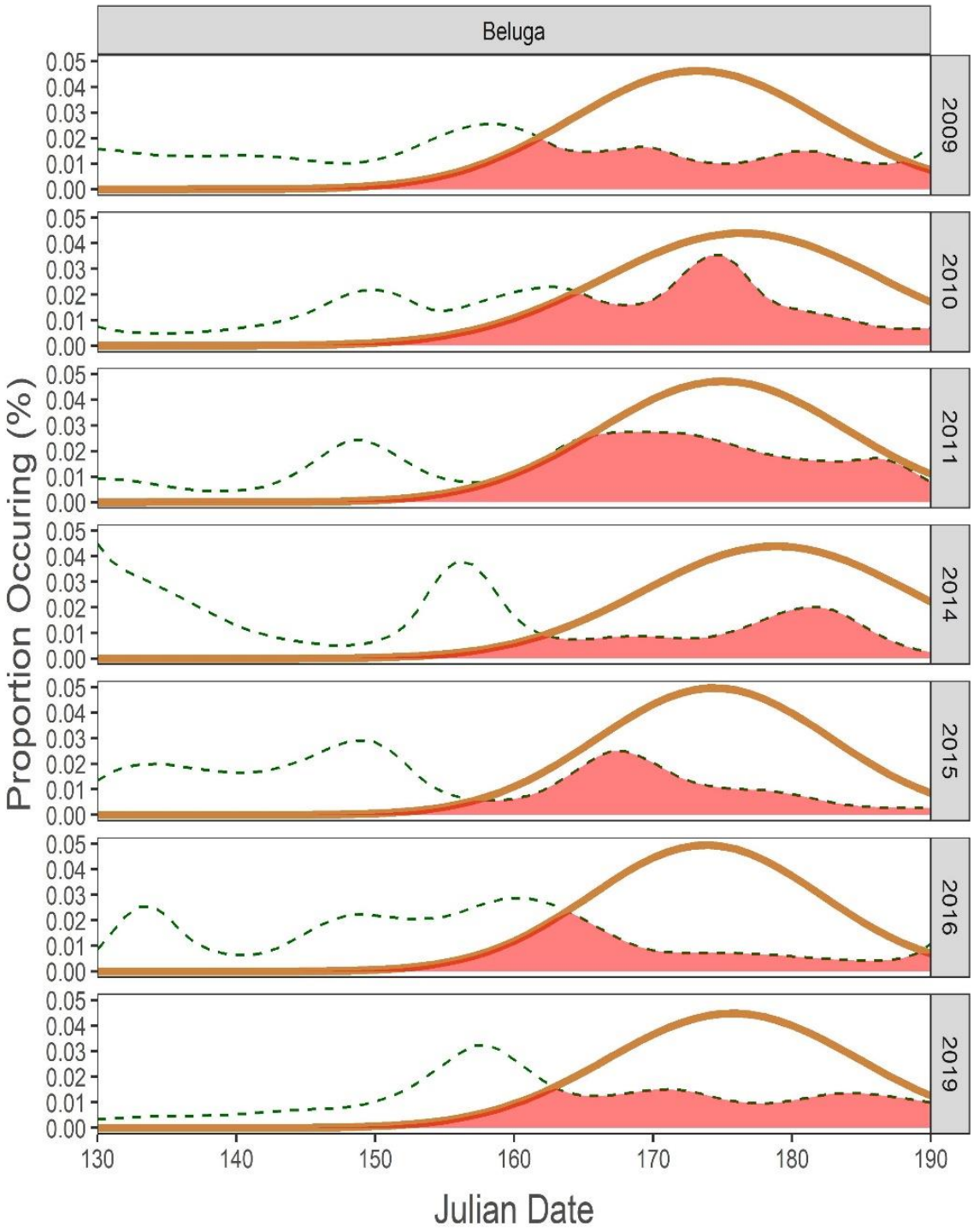


Figure B.4. Overlap of the resource (i.e., daily invertebrate biomass) and Hudsonian godwit chick whole demand (i.e., cumulative energetic requirements; Kilojoules d^{-1}) curves for each year where both invertebrates and chicks were monitored between 2009–2019. Demand (orange, solid line) and resource (black, dashed line) curves are

represented as annual proportions, with the overlapping region (red, shaded) as a measure of ‘matching’. Each tile corresponds to a study year.

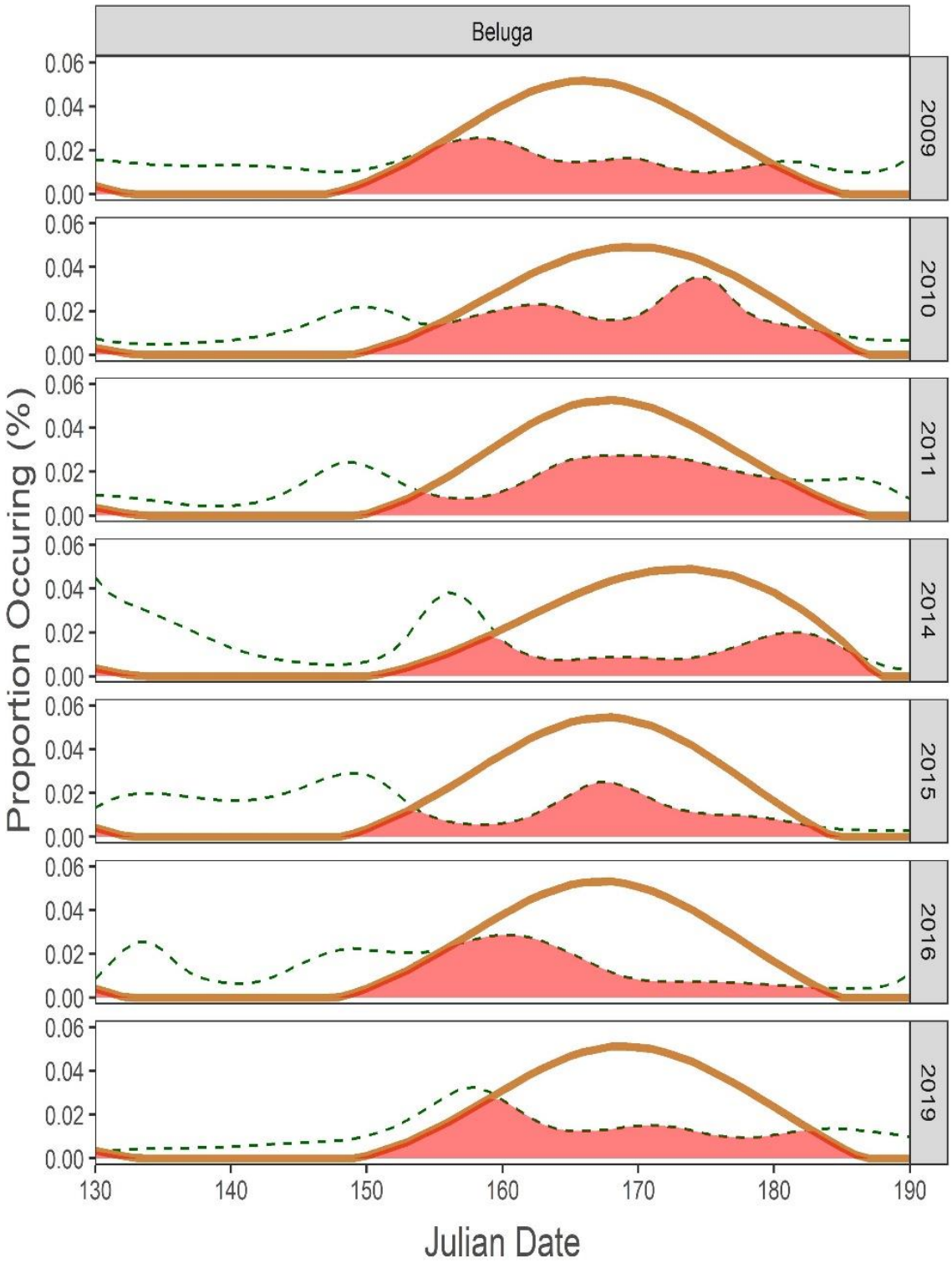


Figure B.5. Overlap of the resource (i.e., daily invertebrate biomass) and Hudsonian godwit chick peak demand (i.e., number of godwit chicks at age of peak growth rate per day) curves for each year where both invertebrates and chicks were monitored between

2009–2019. Demand (orange, solid line) and resource (black, dashed line) curves are represented as annual proportions, with the overlapping region (red, shaded) as a measure of ‘matching’. Each tile corresponds to a study year.